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Heredity of Coat Characters in Guinea-Pigs and Rabbits

BY

W. E. CASTLE
Assistant Professor of Zoölogy, Harvard University
Associate, Station for Experimental Evolution

PUBLISHED BY THE CARNEGIE INSTITUTION OF WASHINGTON,
FEBRUARY, 1905

Carnegie Institution of Washington, Publication No. 23.

Papers of Station for Experimental Evolution at
Cold Spring Harbor, New York. No. 1.

Contributions from Zoölogical Laboratory of Museum of Comparative Zoölogy at Harvard College. E. L. Mark, Director. No. 158.

Press of Gibson Bros.,
Washington, D. C.

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HEREDITY OF COAT CHARACTERS IN GUINEA-PIGS AND RABBITS.

By W. E. Castle.

INTRODUCTION.

The experiments to be described in this paper have been in progress in the Zoölogical Laboratory of Harvard University since the year 1900. They were begun for the study of conditions governing sex in the higher animals, but have yielded results bearing on certain other questions, which alone will be considered in this paper.

The animals used, guinea-pigs and rabbits, were selected because of their early maturity and fecundity. To provide them with food and shelter and to give them the necessary daily care, in addition to keeping records as full as possible, have been no small task. In this connection I am indebted for invaluable assistance to a number of persons. First of all to Prof. E. L. Mark, director of the zoölogical laboratory, without whose encouragement and support the experiments could never have been undertaken, and who has more than once come to the rescue when the material resources at my command were exhausted and further progress seemed impossible. The director and other officers of the Museum of Comparative Zoölogy, and the President of the University, have generously provided quarters for the animals and in other ways have aided the enterprise. Finally, when the increasing cost became a burden too heavy for the laboratory to bear, it was assumed by the Carnegie Institution of Washington in the form of a grant to Professor Mark and myself for experimental studies in heredity. Under the auspices of the Carnegie Institution the work has been in progress since January, 1904, and this paper is presented as a first detailed report upon it.

In the course of the experiments about 3,000 guinea-pigs and several hundred rabbits have been reared.

For valuable guinea-pigs and excellent practical suggestions I am indebted to Miss Jeannette Soule, secretary of the National Cavy Club; for an interesting stock of albino rabbits I am indebted to Prof. R. T.

Jackson. During the academic year 1903–1904, Mr. R. C. Kibbey has given me valuable assistance in the breeding experiments, and Mr. A. D. Howard in the study of the hair pigments.

EXPERIMENTS WITH GUINEA-PIGS.

Heredity of Coat Color.

In the coat of many mammals there occur two or more distinct pigments associated together in the same individual hair, and according as one or the other of these predominates in particular regions of the hair or of the body, a distinct "ticking" of the hair is produced, or a color-pattern of the body. Familiar examples of "ticked" or particolored hairs are those of mice, squirrels, and foxes. Body color-patterns of the sort mentioned occur in cats, tigers, leopards and the like.

In mice Bateson (:03)* has shown that there occur three different pigments—black, chocolate, and yellow. In the wild mouse all these pigments occur together in the same individual hair, but in fancy mice the pigments may occur singly or combined in pairs, when they produce the color varieties most sought by fanciers. Bateson's observations have been confirmed by Allen (:04).

COAT OF THE WILD CAVY.

In wild guinea-pigs (or cavies) occur the same three pigments as in mice, viz, black, chocolate, and yellow. A skin of a young *Cavia aperea* Linn. from Brazil, which lies before me, shows a coloration similar to that of the "agouti" variety of the domesticated guinea-pig. On the back and sides of the body the ordinary hairs have a tip, about 2 mm. long, of a deep brownish-black color. Below this comes a yellow band of about the same length. The rest of the hair appears black, but is less heavily pigmented than the tip, and grows lighter toward its base, which is of a dull leaden color. Microscopic examination shows that the medulla of the hair, throughout its length, contains fine pigment granules of an intense black color, and associated with them others of a chocolate-brown color. The former are much more numerous than the latter, and both are much less abundant toward the base of the hair than at its tip. The cortex of the hair contains throughout the greater part of its length, where it is relatively thin, only some chocolate pigment with a very little black. But in the distal part of the hair the cortex is much thicker and more heavily pigmented. Its terminal 2 mm. has the combination of chocolate and black already described, but in the region just proximal to this it contains only bright yellow pigment, which produces the yellow ticking of the coat.

The longer, so-called contour hairs, found on the back and sides of

* The figures in parentheses refer to the Bibliography, p. 77.

the animal, are black throughout their length, lacking entirely the subapical yellow band. On the lower side of the body the hairs have a pigmentation similar to that of the ticked hairs of the back, but the yellow band is longer and less sharply limited, and the black tip is inconspicuous, so that the fur appears superficially of a dull yellow color, but when parted is seen to be leaden black at the base.

COLOR VARIETIES OF DOMESTICATED CAVY OR GUINEA-PIG.

In the various color varieties of domesticated cavies the same three sorts of pigment found in the wild animal exist singly or in combinations sometimes identical with those found in the wild animal, sometimes different.

AGOUTI.

In the *agouti* variety, of which there are two distinct sub-varieties, known respectively as golden and silver agouti, all three pigments are present, distributed as in the wild cavy. In the *golden* agouti the pigments of all three sorts are abundant and dark, so that the yellow band becomes a red of the sort found in a sorrel horse, while the remaining portions of the hair are fairly deep black. In *silver* agouti the pigmentation is less heavy. It may fairly be described as a dilute condition of the golden agouti. The yellow band is of a pale yellow color, and the black portions of the hair are a pale or bluish black. Silver agouti may be produced by crossing golden agoutis with albino animals of a particular sort, as will be explained presently.

YELLOW.

Yellow-coated varieties, with hair containing neither black nor chocolate pigment, are distinguished according to the depth of their color, as *red*, *yellow*, or *cream*.

In the lighter shades, as compared with the darker ones, the pigment granules are smaller and possibly less numerous. The *skin* covering the feet and ears of animals of this variety contains chocolate pigment, and, at least in some cases, black also; the eye, too, certainly contains chocolate pigment as well as black, yet the hair, as stated, never contains black or chocolate pigment.

CHOCOLATE.

Of the chocolate variety I have made as yet a very incomplete study, for lack of material. The two animals which I have had bore one a spot of red, the other a spot of yellow. Neither bore any black hairs. The chocolate hairs apparently contain no other pigment. Theoretically it should be possible to obtain a chocolate-colored animal entirely free from yellow as well as from black pigment, as is possible with mice (see Allen, :04). My experiments have not progressed far enough to show whether this expectation can be realized.

BLACK.

In the black variety, black pigment predominates over the other two sorts and obscures them. But I have never been able to obtain it in a pure state. Chocolate is invariably associated with it, and usually hairs can be found somewhere on the body which show the presence of the red-yellow pigment also.

In the ordinary black hair chocolate pigment predominates in the cortex, black in the medulla. I am unable to say whether the red-yellow pigment is present with them or not, but I am inclined to think that in some cases at least it is, for here and there on the body one can frequently find a hair devoid of the black and chocolate pigments, and such a hair commonly shows a red or yellow pigmentation. Still there are reasons for supposing that with proper attention a black variety could be produced which would have no red or yellow in its coat, just as red or yellow animals are obtained free from black and chocolate.

The black, like the red-yellow variety, occurs in forms more or less heavily pigmented, the lighter shades being known as *blue*. The latter can be produced by crossing black animals with red or yellow ones, or with albinos of certain sorts. Blue animals bear the same relation to black ones as silver agoutis to golden agoutis. Blue and silver agouti are *dilute forms* of black and golden agouti, respectively. In a blue animal the black and chocolate pigments are less abundant, and the red-yellow pigment, if it appears on separate hairs, is of a light (yellow) shade.

ALBINO.

The albino or white variety, though apparently the simplest as regards pigment characters, is in reality the most complex. Albinos have pink eyes, the color of which is due not to a pigment, but to the blood seen through the transparent eye. The hair is likewise unpigmented at birth, and may remain of this character throughout life over the greater part of the body. Albino mice and ordinary albino rabbits apparently never develop pigment in any part of their coat, but such is not the case in cavies. Though I have carefully sought them, I have never yet seen albino individuals which in adult life did not form pigment in some region or other of their coat. This pigment makes its appearance first and chiefly at the extremities of the body—on the ears, the feet, and the nose—but may in extreme cases extend to the hairs of the body coat also. To the unaided eye the hairs of the extremities are of a sooty black color; the microscope shows them to contain chocolate pigment, with an occasional granule of black.

In the body hairs I have in one case identified reddish-yellow granules without those of other sorts. They are not at all abundant and are found principally at the tip of the hair, so that the coat looks like an

ordinary white one which has become dirty. For a long time I so accounted for the condition seen in a particularly unattractive albino in my flock, but finding that no change occurred in her coat, I investigated the case with the result noted. So-called Himalayan rabbits are albinos with peripheral pigmentation similar to that just described for cavies. But there occur also albino rabbits without peripheral pigmentation. In the Himalayan rabbit, as in the albino cavy, the coat of the young is commonly white at first all over the body, but soon becomes pigmented at the extremities. In some cases the first coat on the general body surfaces is slightly pigmented also, the pigment being found chiefly in the hair tip. This pigmentation is already forming at birth, and can be recognized by the deeper red color of the skin, as compared with that of normal individuals.

I have never seen a case in which this pigmentation of the hair-tips persisted in the adult animal, though that of the extremities regularly does. It is apparently in rabbits restricted to the first coat, though in guinea-pigs it is found only in the later coat.

It is difficult to formulate a satisfactory definition of an albino mammal. Absence of pigment is the most obvious characteristic of albinos; yet, as we have seen, many albinos possess a considerable amount of pigment. Furthermore, experiment shows that black-eyed white cavies, which produce no pigment whatever in the coat, nevertheless transmit very different hereditary pigment potentialities from those of albinos. Accordingly the *amount* of pigment produced in the coat is not distinctive between albinos and other animals; neither is the absence of pigment from the eyes distinctive, for Darbishire (:04) has experimented with a race of pink-eyed mice which when crossed with albinos behave in every way like ordinary pigmented ones.

Without attempting a complete analysis of the matter, for which present knowledge does not suffice, I would suggest the following as criteria which, so far as observed, separate albino mammals sharply from all others. An albino is an animal with unpigmented eyes and with little or no pigment in its coat. The pigment, if present, is found in greatest amount *at the extremities of the body.* In a word, the pigmentation of an albino is essentially *centrifugal.* When by selection or cross-breeding the pigmentation is reduced, it is reduced centrifugally.

But in animals *not* albinos, the pigmentation is *centripetal.* Reduction of the pigmented areas takes place in this case toward well-marked centers, as has been pointed out by Allen (:04) in the case of mice. From a study of spotted mice Allen was led to recognize for that animal five paired pigment centers situated dorso-laterally, as follows: (1) genal or cheek center, (2) nuchal or neck center, (3) scapular or shoulder center, (4) pleural or side center, and (5) sacral or rump cen-

ter. It is possible that we should recognize as a sixth distinct center the retina of the eye. These same centers are recognizable with great clearness in the guinea-pig, for in many cases adjacent patches, when not separated by unpigmented areas, contain elementary pigments whose limits are marked by sharp color contrasts. Thus a cheek patch may be black and the adjacent shoulder patch red (fig. 5);* or the side patch black and the sacral patch red, or *vice versa* (figs. 1 and 3); or again, the right patch of a pair black, the left red, or *vice versa* (figs. 3 and 6). As compared with the mouse, the guinea-pig shows slight differences in the location and extent of the pigment patches, as one might expect

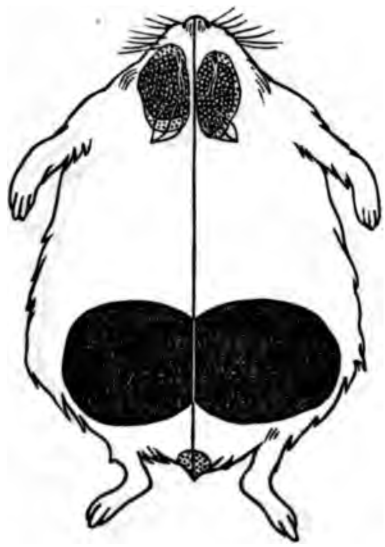

FIG. 1.—Diagram showing the coat pattern of ♀ 973. Cheek, side, and rump patches are present, though much reduced in extent. Each pair is of a different color.

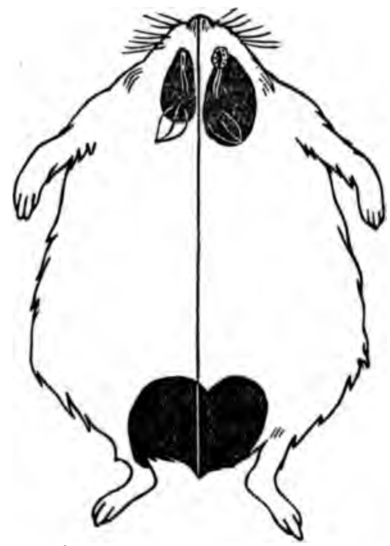

FIG. 2.—Coat pattern of ♀ 2166, a daughter of ♀ 973 (fig. 1). Cheek and rump patches are present, but no shoulder or side patches.

in forms structurally so different. The side patch of the guinea-pig lies chiefly posterior to the middle of the body and frequently extends well back, covering the greater part of the hip and hind leg, while the sacral patches may be so small and closely approximated that they seem to form an unpaired area at the extreme posterior end of the body (figs. 1, 5, and 7). The pigment patches are apparently not correlated with internal structures, such as the distribution of blood vessels or nerves. They are epidermal in origin and subject to more or less apparent asymmetry and mutual displacement, as if they were derived from distinct groups of ectodermal cells endowed in many cases with distinct pig-

* In figs. 1–8, solid black indicates black coat; black stipple, red coat; white stipple on black ground, red and black hairs interspersed.

ment potentialities, which by unequal cell multiplication come to cover areas which may or may not be symmetrical in arrangement.

Sometimes one or both of a pair of patches is wanting altogether; in other cases a patch apparently gets displaced from its normal position, so that it lies across the median plane; frequently when a right or left patch is wanting, its mate extends somewhat beyond the median plane (fig. 3). Nevertheless, when one examines a number of spotted animals it is clear that there is a strong tendency for the pigmented areas to occur in the general body regions indicated, each of the ten recognizable patches being a unit in the composition of the coat.

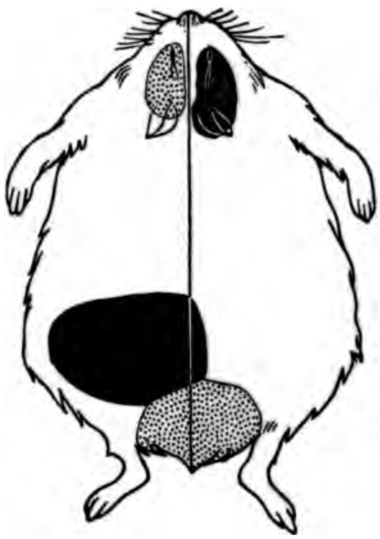

FIG. 3.—Coat pattern of ♂ 1358, a son of ♀ 973 (fig. 1). The right cheek patch is black, the left one red. There is a left side patch of black, but no right side patch. The fused rump patches are red.

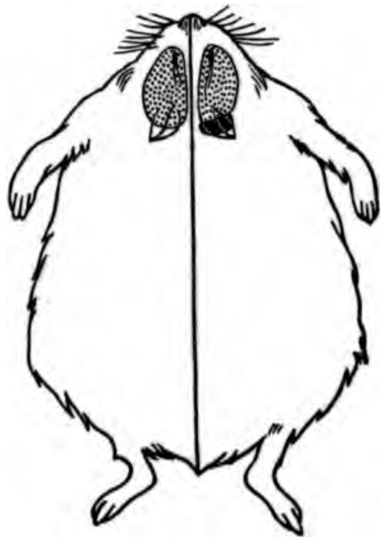

FIG. 4.—Coat pattern of ♂ 1360, a son of ♀ 973 (fig. 1). There are cheek patches of red, and a right neck (ear) patch of black. No others of the typical patches are present.

This unity may be obscured if it happens that two pigments, as black and red for example, are both present in the same patch. Nevertheless, in such cases one can often still identify the typical patches either by the occurrence of unpigmented areas between them, or by the occurrence of mixed pigments in one patch and of unmixed pigments in adjacent patches.

At one time I thought that I had obtained an explanation of the difference in behavior of the centrifugal and centripetal types of pigmentation. It seemed that the centrifugal pigmentation was of dermal origin, the centripetal of epidermal origin; but more careful examination of sections of the skin indicates that both sorts of pigmentation are similar in origin, arising within cells of the epidermis.

SPOTTED.

The five principal color varieties of the cavy which have thus far been described are alike known as self-colored (*i. e.*, colored alike all over), in distinction from the spotted or pied varieties, which will next be noticed. Each of the four varieties, agouti, black, chocolate, and yellow (including red), may become spotted with white either by reduction in the extent of the pigment patches (as already explained), so that they no longer meet and cover the entire body, or by the entire absence of one or more of the typical color patches. The first-named process produces such familiar manifestations of partial albinism as (1)

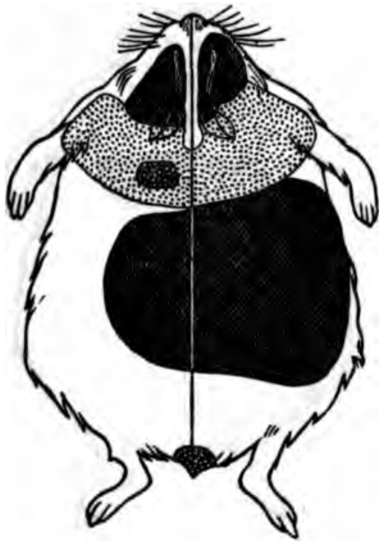

FIG. 5.—Coat pattern of ♂ 2698. The cheek patches are of black, the combined neck and right shoulder patches red; in the corresponding area of the left side are a few black hairs mixed with the red; the side patches are black, the minute rump patch mixed red and black.

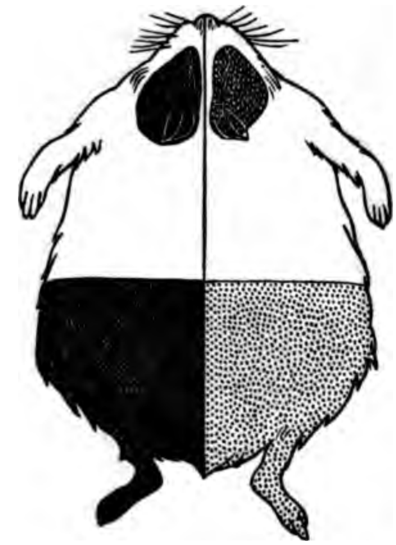

FIG. 6.—Coat pattern of ♀ 1920. The left cheek patch is black, the right one red and black mixed. The right side and rump patches are red, the left ones black. A sharp line of division separates them along the median plane both dorsally and ventrally.

a white spot or a longitudinal white streak on the belly of the animal, where the side or shoulder patches fail to meet below, or (2) a white throat, where the cheek patches fail to meet below, or (3) a white blaze (forehead stripe) where they fail to meet above (fig. 5), or (4) white feet, to which the shoulder and rump patches do not quite extend. Dropping out of one or more entire pigment patches may produce an asymmetrical white spotting, such as a white cheek, shoulder, or side. The two processes, reduction in extent of the pigment patches and dropping out altogether of certain pigment centers, usually progress simultaneously, and when they occur symmetrically may result in such

forms as the much admired Dutch-marked varieties, in which the two cheek patches are distinct (not united) above and below, the shoulder patches are wanting altogether, leaving a broad white girdle around the animal, and the rump patches fail to reach below the middle of the hind leg, though united dorsally (compare fig. 6, which shows an approximation to the Dutch-marked type).

A mottling similar in pattern, but with different color effects, is produced when the various patches are differently colored. Thus in one strain which I have bred from the beginning of my experiments, some of the pigment patches are usually pure black, others pure red, though

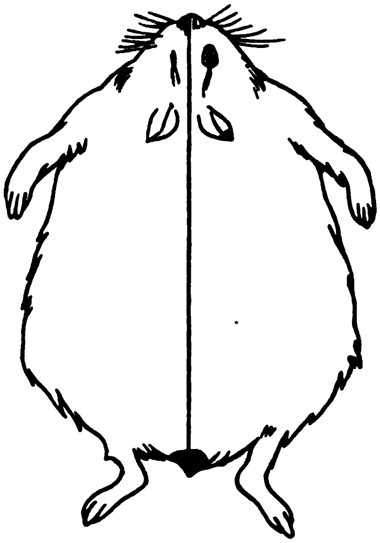

FIG. 7.—Color pattern of ♀ 2427. The color patches are of very limited extent. They consist of a red eye patch and a black neck (ear) patch in the right half of the body, and a median (paired, but fused?) rump patch.

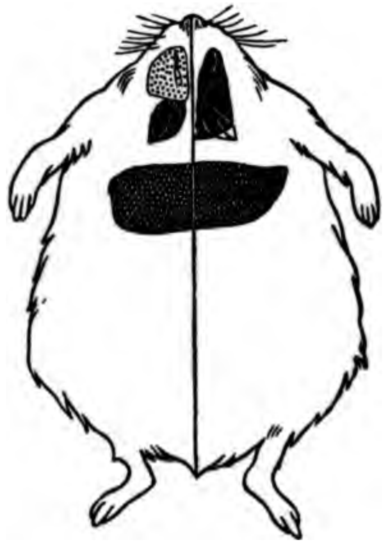

FIG. 8.—Color pattern of ♀ 2928. The left cheek patch is red, the adjacent neck (ear) patch black. The fused right cheek and ear patches are black. The fused shoulder patches are of mixed red and black.

occasionally a patch contains hairs of both colors intermingled. (See figs. 1–8.) Further, the patches in this strain frequently fail to cover the whole body, so that the animals are mottled with large clear areas of black, red, and white, a condition which undoubtedly has been common among domesticated cavies since their introduction into Europe from South America some three or more centuries ago. (See Cumberland, p. 11.)

BRINDLED.

In brindled animals black and red hairs are interspersed in the same pigment patches. The latter may or may not be continuous with each other; if they are not continuous, white mottling results, associated with the brindled character.

ROAN, AND SILVERED.

In roan animals white hairs are interspersed with red ones. A similar modification may occur in the coat of black animals also, which are then said to be "silvered." I have never seen a cavy with an entire coat of this character; usually certain patches only are affected, or more often the ventral part only of a patch. I have noticed, however, the transmission of this character from generation to generation and have no doubt that a roan race or a silvered one could be established if desired.

RESULTS OF CROSSING THE ELEMENTARY COLOR VARIETIES.

ALBINOS AND PIGMENTED ANIMALS.*

These two types are very distinct. Each by itself breeds true, and cross-breeding between them fails to produce intermediates; it results invariably in the production of young of the centripetally pigmented type. Thus in the course of these experiments, (1) albino parents mated *inter se* have produced 156 young, all albinos; (2) pure pigmented parents (*i. e.*, animals altogether devoid of the albino character) mated *inter se* have produced 261 young, all pigmented; and (3) albinos mated to pure pigmented animals have produced 314 young, all pigmented. The young produced by this last sort of mating, though similar in appearance to those produced by (2), are not *pure* pigmented animals, for they possess the potentiality to form albino young, which the young of the two pure pigmented parents do not. In Mendelian† terminology the pigmented character is *dominant*, the albino character is *recessive*, and cross-breds between a dominant and a recessive parent are *hybrid dominants*. The hybrids form gametes (*i. e.*, spermatazoa and eggs ready for fertilization), half of which, approximately, transmit the pigmented character, half the albino character.

Students of heredity at the present time are giving earnest attention to testing the two principles which make up Mendel's law, viz, (1) the principle of dominance, and (2) the principle of segregation. In the case under consideration there can be no question of the validity of both. The centripetal type of pigmentation invariably dominates over the albino, as the statistics already given clearly indicate. This is in harmony with numerous observations on mice, rats, rabbits, and other mammals made by Haacke ('95), Von Guaita ('98, :00), Cuénot (:03, :04),

* Although, as we have seen, the albino guinea-pig regularly develops a certain amount of pigment in its coat, it will be convenient to use the term "albino" in contrast to "pigmented," the latter term referring only to the dark-eyed centripetally pigmented animals.

† For a brief statement of Mendel's law, see Castle (:03, or :03a); for a fuller one see Bateson (:02).

Darbishire (:04), Castle & Allen (:03), Bateson (:03), Allen (:04), and others. The evidence that segregation of the dominant and recessive characters occurs when the cross-bred pigmented animals form gametes is not less clear. The matter can be conveniently tested in two ways: (1) By mating a cross-bred with an albino animal, when half the young should be pigmented, the other half albino, if segregation occurs as demanded by Mendel's law; (2) by mating hybrids *inter se*, when we should expect three-fourths of the young to be pigmented, one-fourth albino. The first sort of mating has in these experiments produced 211 pigmented and 214 albino young, where the expectation is 212.5 of each sort, which certainly is a very close approximation. The second sort of mating has produced 264 pigmented and 112 albino young, the expectation being 282 pigmented and 94 albino young, *i. e.*, there are 18 more than the expected number of albinos in a total of 376 young, a fairly close approximation, but not so close as that observed in the first case.

Combining the results of all matings which are expected to produce albinos, we get the following:

	Pigmented.	Albino.
Expected...........	494.5	306.5
Observed...........	475	326

This shows an excess over expectation of 19.5 albinos in a total of 801 young, or about 2.5 per cent.

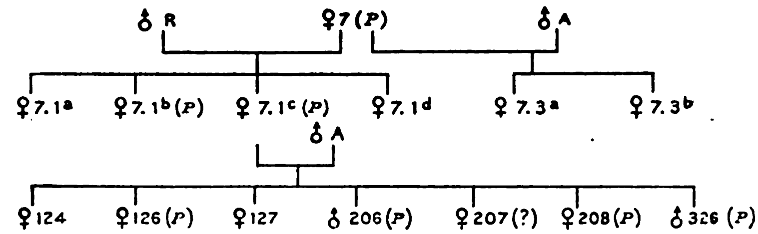

FIG. 9.—A genealogical table showing the character, as regards recessive albinism, of the young produced by three matings between a pure pigmented (*P*) and a hybrid pigmented animal.

Matings of hybrid pigmented with pure pigmented animals have, as expected, produced only pigmented offspring, which number 351. The Mendelian expectation is that half the young so produced will be *pure* in character, half *hybrid*. Since the two sorts look alike, only individual breeding tests will suffice to distinguish them. In certain cases such tests have been made, the results showing that the expectation based on theory is realized.

Fig. 9 shows the results of three different matings of this sort in a single

family of guinea-pigs. The animals enumerated were all pigmented; those marked (*P*), when mated with albinos, produced only pigmented young showing that they were *pure;* the others produced some albino offspring, when mated with albinos (or with other hybrid pigmented animals), showing themselves to be hybrid in character. In the case of one animal only (♀ 207) no test was made as to the production of albino gametes. This animal was paired with pure pigmented mates only, and the young were, of course, invariably pigmented.

It will be observed from fig. 9 that pure ♀ 7 was mated with two different hybrid males, viz, ♂ R and ♂ A. By ♂ R she had four daughters (♀ 7.1^a, ♀ 7.1^b, ♀ 7.1^c, and ♀ 7.1^d), two of them pure (*P*), two hybrid in character. By ♂ A she had two daughters (♀ 7.3^a and ♀ 7.3^b), both hybrid in character. In the next generation, hybrid ♂ A was mated with pure ♀ 7.1^c, producing in three different litters seven pigmented young, which were used as breeders. One of these (♀ 207) was not tested for recessive albinism, as already stated. Of the others, four proved to be pure, two hybrid in character. Altogether there were among the young indicated in the table six pure individuals, six hybrids, and one of uncertain character.

So far as observed, there are no intermediate conditions between pure and hybrid pigmented animals. If an animal forms albino gametes at all, *half* its gametes are of that character. Of course in individual litters, or when only small numbers of offspring are dealt with, considerable deviations from the Mendelian ratios are likely to be encountered. This is to be expected on the theory of probabilities, as Allen (:04, p. 110) has clearly pointed out. But when more extensive tests are made the expected ratios are more closely approximated.

ALBINISM AND THE "LAW OF ANCESTRAL HEREDITY."

The foregoing results show very clearly that albinism conforms in its mode of inheritance to Mendel's law of heredity. The fact, however, must not be overlooked that a somewhat different explanation of its inheritance has recently been given, based on Galton's "law of ancestral heredity." I shall not at this time enter into a detailed discussion of Galton's hypothesis, which was an entirely rational one in the form in which it was originally proposed, and quite in harmony with the phenomena of gametogenesis as then interpreted. I have shown elsewhere (Castle, :03^b) by a specific test in the case of mice, based on the observations of Von Guaita ('98, :00), that Galton's law fails to account for the observed facts concerning the inheritance of albinism, but that Mendel's law does this perfectly. Nevertheless Darbishire (:04), likewise dealing with albinism in mice, though admitting that certain of his results are not in disagreement with Mendel's law, is inclined rather

to interpret the phenomena on some such hypothesis as that of Galton. He states the matter very clearly (p. 24) as follows:

It is well known that according to this [Mendelian] view the hybrid contains equal numbers of germ-cells which produce the dominant character, and of those which produce the recessive; and this is said to be true of the hybrids however far the individual is removed from the original cross, whether it is the result of the cross (*i. e.*, the hybrid) or the great-great-grandchild of this. This is the ground on which the doctrine of the purity of the germ-cells and the law of ancestral heredity flatly contradict one another; the former asserting that $DR \times DR$ will produce 25 per cent DD, 50 per cent DR, and 25 per cent RR for a very great if not an indefinite number of generations; the latter maintaining that the further the individual hybrid under consideration happens to be removed from the cross the less albinos will it produce; and that two hybrids whose mothers were albinos will produce more albinos than would two hybrids who have no albinos in their pedigree later than their great-great-great-grandmother. This seems to me to afford a case in which experiment could provide a decisive answer.

In this statement I heartily concur.

The experiment which Darbishire made was this. He made three different kinds of matings between animals which, we are told, were hybrids. (1) In one case each of the two animals mated had one albino and one pigmented parent. (2) In the second case, one animal was of the parentage just described, the other was born of two pigmented parents. (3) In the third case, the parents of both animals were pigmented. In brief, there were *two* albino grandparents in case (1), *one* albino grandparent in case (2), and *no* albino grandparents in case (3). The ancestry back of the grandparents was the same in all three cases. The conditions are thus very simple and should, as Darbishire suggests, give a decisive test. Darbishire states that—

	Number of young.	Number of albinos.	Albinos (per cent.).
Mating (1) gave....................	121	30	24.79
Mating (2) gave....................	107	20	18.69
Mating (3) gave....................	93	10	10.75

This is a seemingly conclusive demonstration of the correctness of Darbishire's contention; but in fact Darbishire's results, when carefully analyzed, prove just the opposite of his deduction.

Fortunately he has recorded in an appendix the various litters from which the totals given are made up. An examination of these records makes it evident that his so-called "hybrids" were no[t]
In mating (1) the animals used undoubtedly were h[ybrids]
had, as stated, one albino and one pigmented parent
that in that case the Mendelian expectation of

realized as perfectly as is possible in an odd number of young, there being 30 albinos in a total of 121 young. In cases (2) and (3) Darbishire gives us no evidence that the animals which he mated were really hybrids in the sense that they contained recessive albinism. He calls them "extracted hybrids" because they had dark eyes, as did all his *primary* hybrids obtained by crossing pink-eyed with albino mice. The latter unquestionably were hybrids in the sense that they contained recessive albinism, for in every case one of the parents was an albino. The former may or may not have contained albinism recessive; Darbishire's experiments indicate that in some cases they did, and in other cases they did not. Darbishire himself has shown that there is in his mice (contrary to an erroneous prediction of Castle & Allen, :03, p. 612) no necessary correlation on one hand between recessive albinism and dark eyes, and on the other hand between freedom from albinism and the pink-eyed pigmented-coat condition. He calls especial attention to the fact (p. 22) that in five different families of his mice there occurred altogether seven pink-eyed pigmented animals, which in each case had one albino and one pigmented parent, and which accordingly must have been hybrids. In an earlier paper (Darbishire, :03, p. 285) he showed that a pink-eyed mouse of this kind does produce albino offspring when mated to albinos, a thing which his original (pure) stock of pink-eyed mice never did. If, then, pink-eyed pigmented animals may contain recessive albinism, is it improbable that dark-eyed animals may in some cases *fail* to contain it?

Accordingly, in what have been called Darbishire's matings (2) and (3), we may reasonably ask for evidence that the animals mated were really hybrids. A pair which has produced albino offspring consists unmistakably of two hybrid animals. Pairs which fail to do this are questionably hybrid and may be provisionally left out of consideration. In mating (1) where both parents were unquestionably hybrid, since each had an albino parent, Darbishire gets the precise Mendelian proportion (one-fourth) of albinos. The question is, are fewer albinos produced by hybrids in matings (2) and (3), in which the albino ancestry was less.

Omitting only pairs which failed to produce *any* albinos in matings (2) and (3), Darbishire's observations may be summarized as follows:

	Pigmented young.	Albino young.	Albinos (per cent).
Mating (1)	91	30	24.79
Mating (2)	44	20	31.25
Mating (3)	35	10	22.22
Matings (2) and (3) together.	79	30	27.52

Instead of producing *less* than 25 per cent of albinos, as Darbishire supposes them to do, matings (2) and (3) really produce *more* than that proportion of albinos. Considered separately they produce, one somewhat more than 25 per cent, the other somewhat less, as we should expect to be the chance result where small numbers of young are considered.

In further evidence that Darbishire's "extracted hybrids" did not in all cases contain recessive albinism, his matings of such animals with albinos are instructive (see his Table F, p. 36). Five out of nineteen such matings failed to produce *any albinos whatever*, though they produced a total of 19 young, all pigmented. If the pigmented parents in these matings had really been hybrids, half their young should have been albinos. Such was precisely the proportion of albinos produced by the fourteen matings in which the pigmented parent, though of the same ancestry as in the foregoing cases, showed itself to be really a hybrid, for these fourteen matings produced 36 pigmented young and 36 albinos.

Darbishire designates the cases just discussed "the most conclusive results which I have obtained" [in favor of the law of ancestral heredity]. Careful examination of these results, however, as we have seen, makes them seem far from conclusive in favor of that hypothesis. I have, therefore, thought it worth while to apply a further experimental test to Darbishire's hypothesis, in the case of guinea-pigs.

In doing so I class as a hybrid pigmented animal (1) any pigmented animal known to have had an albino parent, or (2) any pigmented animal born of pigmented parents which has produced one or more albino young. In Tables A and B are summarized the results of all of the matings between two animals known to be hybrids, or between a hybrid and an albino, which have been made in my later experiments. Matings from my earlier experiments are not included for the reason that the ancestry of the animals at that time used is too imperfectly known. The Mendelian expectation is, as Darbishire states, that all hybrids alike, whether they have few or many albino ancestors, will form gametes approximately half of which bear the albino character, half the pigmented character. Darbishire's contention, on the other hand, based on the hypothesis of Galton, is that the more albino ancestors a hybrid animal has, the more albino offspring will it produce. To test these alternative hypotheses I have tabulated the matings which have been made in these experiments according to the amount of albino ancestry involved in each, this amount being greatest in the first part of each table. Table A includes matings between two hybrids, Table B matings between a hybrid and an albino.

TABLE A.—*Proportions of albino young produced by hybrid pigmented parents of different amounts of albino ancestry.*

Albino grand-parents.	Albino great-grand-parents.	Albino young.	Pigmented young.	Remarks.
2	6	3	13	Two albino grandparents, 43 albino to 124 pigmented young, or 25.9 per cent. albinos.
2	4	9	28	
2	3	3	4	
2	2	11	28	
2	0	17	51	
1	4	5	1	One albino grandparent, 16 albino to 18 pigmented young.
1	3	3	4	
1	1	5	7	
1	0	3	6	
0	1	1	3	No albino grandparents, 6 albino to 16 pigmented young.
0	0	5	13	
...	...	65	158	

TABLE B.—*Proportions of albino young produced by matings between albinos and hybrid pigmented animals, both with varying amounts of albinism in their ancestry.*

Albino grand-parents.	Albino great-grand-parents.	Albino young.	Pigmented young.	Remarks.
3	7	1	3	Three albino grandparents, 55 albino to 64 pigmented young.
3	6	24	35	
3	5	5	6	
3	4	10	9	
3	3	4	2	
3	2	3	1	
3	1	3	1	
3	0	5	7	
2	6	1	3	Two albino grandparents, 63 albino to 56 pigmented young.
2	5	8	3	
2	4	21	20	
2	3	8	8	
2	2	16	15	
2	0	9	7	
1	5	0	3	One albino grandparent, 13 albino to 18 pigmented young.
1	2	4	3	
1	1	2	3	
1	0	7	9	
0	3	2	4	No albino grandparents, 5 albino to 10 pigmented young.
0	0	3	6	
...	...	136	148	

Throughout Table A we find the expected Mendelian ratio (1 : 3) of albino to pigmented young approximated, quite irrespective of the amount of albino ancestry back of the parents mated. Of course, there are marked deviations in individual cases where the number of young

is small, as we expect on the theory of probabilities, but we find no falling off in production of albinos as the amount of albino ancestry decreases.

Similarly throughout Table B we find the expected Mendelian equality of albino and pigmented young approximated, irrespective of the number of albino grandparents and great-grandparents. Thus the proportion of albinos is actually higher when there are only two than when there are three albino grandparents, though on Darbishire's hypothesis we should expect this relation to be reversed; for the young produced in cases where there are *three* albino grandparents aggregate 55 albino to 64 pigmented animals, an excess of 4.5 pigmented; but the young produced in cases where there are only *two* albino grandparents (in the same total number of young) aggregate 63 albino to 56 pigmented animals, an excess of 3.5 albinos. The deviations from equality are in the two cases opposite in character and almost equal. Undoubtedly it is merely a chance outcome that they are opposite in nature to what Darbishire's hypothesis demands. The tables as a whole, however, do give an emphatic negative to Darbishire's position. They lend support to the alternative (Mendelian) hypothesis, that any pigmented animal which forms albino gametes forms approximately 50 per cent of such gametes.

In what precedes I have made no mention of what has been called Pearson's modification of Galton's law of ancestral heredity. Elsewhere (Castle, : 03[b]) I have discussed this briefly in applying a statistical test to the laws of Galton and Mendel in the case of albinism in mice. Galton's law I applied generation by generation to Von Guaita's ('98, : 00) mouse records, as Galton ('97) himself had applied his law to the Basset hound records. The test thus made showed the complete failure of Galton's law as applied to the heredity of albinism. No such detailed test was made in the case of Pearson's law, but the statement was made: "Comparing Pearson's series with that of Galton we see that the parental influence is reckoned as substantially the same by both Galton and Pearson, but that Pearson assigns a much greater influence to the more remote ancestors than does Galton." For which reason it was concluded, "The discrepancies noted between observed and calculated [in testing Galton's law] will remain and even be accentuated if we replace Galton's series with one of those suggested by Pearson. For the result will be unchanged [I should have said similar, rather than unchanged] in Generation II, but the calculated numbers will in most cases diverge still more from the observed ones, in the later generations, because Pearson attaches more weight to the remoter ancestors than does Galton." To these conclusions Pearson (: 04) takes exception, maintaining that neither of the two series which I took from his writings was quoted in a form comparable with that of Galton's series.

He gives a series of his own and that of Galton in comparable form. They are, he says, "if we measure parental influence by intensity of *correlation*":

Influence.	Pearson's series.	Galton's series.
Parental............................	$\frac{1}{2}$	$\frac{1}{3}$
Grandparental......................	$\frac{1}{3}$	$\frac{1}{9}$
Great-grandparental............	$\frac{2}{9}$	$\frac{1}{27}$
Great-great-grandparental....	$\frac{4}{27}$	$\frac{1}{81}$

Even when they are given thus, it seems to me still, as I stated before, that "Pearson attaches more weight to the remoter ancestors than does Galton," and if so, that "the discrepancies noted between observed and calculated [in testing Galton's law] will remain and even be accentuated if we replace Galton's series with one of those suggested by Pearson." That Pearson himself had not contemplated such a test of his law would not affect in the slightest degree the outcome of the test. Further, it seems to me an admission very damaging to a law of heredity when Pearson says: "Personally I. have no means of determining whether the law of ancestral heredity holds or does not hold for coat color in mice. The theory has not yet been worked out in a form covering Von Guaita's cases." Yet in Von Guaita's material we have a full record of the coat color of every animal in seven successive generations, and we know that back of this for an indefinite number of generations all the ancestors on one side of the ancestry were albinos, on the other side spotted black-and-white. That is sufficient basis on which to make very reliable predictions as to the character of the offspring, under Mendel's law, as I have elsewhere shown.

In fact, it seems to me that Pearson's law, as he now explains it, is ***not a law of heredity at all***, but one of variability in successive generations, for he says (p. 110): "So far as I can understand the Law of Ancestral Heredity as I have myself enunciated it, the produce of a grey mouse and a fawn mouse might be on the average a green mouse without that Law having anything to say on the point. From it you can not possibly deduce what number of the offspring of any generation will be like this or that ancestor. It is not a law of types, but of the distribution of deviations from type, and this is a very different thing indeed." But from a genuine law of heredity, such as that of Mendel, one is enabled, as I have shown, to predict with great accuracy what color types will prevail among the offspring in successive generations. Since Pearson's law, as now interpreted by its author, though dealing with alternative color types in successive generations, gives no informa-

tion whatever as to *what* color types will prevail in one as compared with another, nor as to what proportion of the young will be *devoid* of color, it would seem desirable, to avoid confusion, that the law be renamed as something other than a law of heredity.

ALBINISM AND SEXUAL PREPOTENCY.

Galton ('97), on purely empirical grounds, was inclined to think the male sex prepotent in the transmission of black spots in the case of Basset hounds. Though I have elsewhere (Castle, :03[b]) shown that the conclusions which he drew from that study were probably erroneous because they rested on false assumptions, it may be worth while in this connection to test the idea of sexual prepotency in regard to albinism. This may be done by comparing the results of reciprocal matings, as shown in Table C, which contains a summary, as regards the production of albino young, of most of the matings made up to this time. Only matings between pigmented parents of undetermined character as regards recessive albinism have been omitted from this summary. These omitted matings produced several hundred young, all pigmented, as was to be expected if either one or both pigmented parents were free from recessive albinism. From Table C it is evident that, (1) when a mating is made between a hybrid pigmented and a pure pigmented animal the result is the same whether the hybrid be father or mother; in every case the young are pigmented; (2) when a mating is made between a hybrid pigmented animal and an albino, hybrid pigmented and albino young are produced in approximately equal

TABLE C.—*Proportions of pigmented (p.) and albino (a.) young produced by matings of various sorts.*

Mothers.	Father pure pigmented.	Father hybrid pigmented.	Father albino.
	Young.	Young.	Young.
	p. : *a.*	*p.* : *a.*	*p.* : *a.*
Pure pigmented	261 : 0	215 : 0	205 : 0
Hybrid pigmented	136 : 0	264 : 112	120 : 116
Albino	109 : 0	91 : 98	0 : 156

numbers, viz, 120 pigmented to 116 albino young when the albino parent was a male, 91 pigmented to 98 albino young when the albino parent was a female. The deviations from equality are very slight and unquestionably the result of chance. In the one case the deviation is 2 individuals in a total of 236; in the other, it is 3.5 in a total of 189 young. There is, accordingly, in this case no evidence of prepotency in the transmission of albinism on the part of either sex.

ALBINISM AND LATENT PIGMENT CHARACTERS.

Although, as we have seen, (1) albinism is a condition recessive in heredity with respect to ordinary or centripetal pigmentation, and (2) albinos produce only albino offspring, irrespective of their ancestry, it is not true, as might be supposed, that one albino breeds like another when *crossed* with the same centripetally pigmented type. This matter has been very fully discussed by Allen (:94, p. 130), but may be illustrated by some simple examples. (1) My albino guinea-pig, ♂ 2002, when mated with red females, invariably produces offspring marked with *black* as well as with red pigment. (2) Albino ♂ 635, when mated with the very same or with similar red females, produces young about half of which are pigmented with black and red, like the offspring of ♂ 2002, the other half being pigmented only with red or yellow, not with black. (3) Albino ♂ 1999, when mated with red females, produces only red (or yellow) pigmented offspring, never black pigmented ones. From an inspection of these three albino males or of their offspring by albino females, one would get no inkling of the existence among them of the differences revealed by the experiment described. This experiment shows that in the gametes produced by ♂ 2002, the capacity to form black pigment is latent. This capacity is exercised whenever such a gamete unites with one bearing the centripetal type of pigmentation. In ♂ 635 only about *half* the gametes formed contain latent black; in ♂ 1999 *none* of the gametes formed contain latent black. The idea underlying this explanation is that a recessive character (in this case albinism) may contain the dominant one (centripetal pigmentation) in a state of inactivity which nothing but cross-breeding with the pigmented type will disturb. Further evidence in support of this idea will be adduced when we come to discuss coat characters other than those of pigmentation.

Meanwhile, let me say a word concerning the term *latency*. In common with others I have frequently in earlier papers used this word loosely as synonymous with recessive. This usage was, I believe, an unfortunate one; accordingly, in what follows I shall use the two terms for conditions quite distinct, which my experiments show to have a real existence and to require names. (1) *Recessive* I shall use as Mendel used it, to designate a character which disappears when brought by fertilization into the same (hybrid) individual with a contrasted "dominant" character, but which is transmitted, distinct from the dominant character, in half of the gametes formed by the hybrid individual. (2) *Latency*, as I shall use it, is a condition of inactivity in which a normally dominant character may exist in a recessive individual or gamete. It is questionable whether a *recessive* character

may ever be latent. Future investigations alone can decide this point. A *recessive* character apparently reappears pure in half the gametes formed by the hybrid dominant individual, and is present in *all* the gametes formed by a recessive individual; a *latent* character apparently *never* regains its existence apart from the recessive (*i. e.*, becomes active) until cross-breeding brings this about. Future investigations may require further modification or even entire abandonment of these definitions, but for the present I find them useful to express the results of my experiments.

Latency of pigment characters in albinos is particularly clear in mice, as shown by the investigations of Cuénot (: 03), Darbishire (: 04), and especially of Allen (: 04). For albino mice are, so far as known, wholly unpigmented, yet they ordinarily, perhaps always, transmit latent pigment characters, either singly or in combinations identical with those occurring in pigmented mice. Alike in guinea-pigs and in mice, a clew to what pigment characters are latent in the individual may often, though not always, be learned from a mere knowledge of its parentage. Thus, in guinea-pigs, an albino born of two red or yellow parents does not transmit latent black in any of its gametes; but one born of two black parents may or may not form gametes transmitting red apart from black pigment. The reason for this difference will be apparent when we come to consider the relation of red and black to each other in cross-breeding. For the present I would merely call attention to this case as showing that it is not the *ancestry* of the albinos which governs the behavior of their gametes in cross-breeding, as Darbishire (: 04) maintains, but rather the existence of pigment characters as distinct entities, though latent, in the gametes formed by albinos. In certain cases we can, with confidence, predict the absence of a pigment character, even in a latent condition, from the gametes of an albino, viz, in cases where we know the pigmented parents to have been free from that character. Thus an albino born of red or yellow parents does not transmit black, because red or yellow animals do not contain the black character either active or latent, and so can not transmit it to their albino offspring. Where the parentage is unknown, suitable breeding tests show with equal certainty (often the production of as few as two young indicates clearly) what latent pigment characters are transmitted by the albino. A particular pigment character, when present latent in the gametes formed by an albino, appears to be regularly present either (1) in *all* the gametes formed, or (2) in *half* those formed, as suggested by the cases of albino ♂♂ 2002 and 635 already cited. No evidence exists of the occurrence of a latent pigment character in other proportions of the gametes, as should be the case on the "ancestry" idea of Darbishire.

INTERCROSSING OF DIFFERENT PIGMENT TYPES.

Intercrossing of elementary pigment types other than albino results not in perfect dominance of one and complete disappearance (recessiveness) of the other, but in coexistence of the two in the offspring, though one pigment character from its nature may be much more in evidence than the other. Thus black animals mated with red ones ordinarily produce black offspring, though of a shade different from that of the black parent, the more intense black pigment masking to a great extent the presence of red. True Mendelian dominance, then, is wanting in such crosses; nevertheless the other Mendelian principle, segregation, is here realized.

THE AGOUTI TYPE.

An agouti animal, as we have seen, is one which bears the three pigments—black, chocolate, and red-yellow—in a particular regional distribution on the same hair. It is the original or wild type of pigmentation and might be expected to show superior potency in crosses. My experiments, which, however, are far from complete, indicate that this type of pigmentation as transmitted in the gametes of a wild animal really is potent over other types. Thus, a male *Cavia aperea*, which was captured wild in southern Brazil, has produced by two different domesticated albino females (neither of which was of agouti-colored parentage) 15 young, all agouti-colored, but in some cases at least of a somewhat lighter shade than the wild parent. I can not speak very emphatically as to the exact shade of pigmentation in several cases, because all but four of the hybrids were born dead, and their coats have been examined as yet only in a wet condition. This matter will be discussed more fully in a subsequent paper.

The agouti type of pigmentation, when borne by gametes of a domesticated guinea-pig, likewise shows a strong tendency to dominate over other types of pigmentation, the only possible exception thus far observed being black.

Agouti × *agouti*.—It goes without saying that pure agoutis, like pure* animals of any other type, breed true. Thus, agouti ♂ 2017 mated with agouti ♀♀ 2019 and 2021 produced 6 young, all of the same (golden) agouti type as the parents.

Agouti × *black*.—Agouti ♀ 2018 mated with black ♂ 2053 (known by test to be pure) produced 3 young, of which one was an agouti, the other two black. This outcome indicates that the black type of pigmentation may in some cases at least have equal potency with the

* The term *pure* is here used, as throughout this paper, in the Mendelian sense, referring to the character of the gametes which an animal forms. Thus a pure agouti animal is one which forms gametes all of which transmit the agouti type of pigmentation.

agouti, showing *alternative* dominance with respect to it. When this result was obtained I at once questioned the purity of ♀ 2018, suspecting that she might contain recessive black, but her purity has since been established with considerable probability by a mating with albino ♂ 635, neither of whose pigmented parents was an agouti. This mating produced 4 young, all agouti or agouti spotted with red. Previously ♀ 2018 had been mated with agouti ♂ 2017, producing 3 agouti young.

Further support for the idea that agouti and black may show alternative dominance is afforded by matings of hybrid agouti (albino)* ♀ 2020. This animal contained recessive albinism in which black apparently was latent. For, when mated with agouti ♂ 2017, she produced 2 agouti and 2 black young, indicating that at least half her gametes bore the black character, and that this dominated over agouti in at least two out of four cases. When mated with albino ♂ 2039 she produced 1 albino, 1 spotted white >† red-black, and 1 spotted red-black young. Mated with hybrid red (albino) ♂ 1019, she produced 2 black > red young. Manifestly only part, if any, of this female's gametes bore the agouti character, though all apparently bore the character black, either in the agouti combination or in the segregated state.

Again, an agouti daughter of ♀ 2020 by agouti ♂ 2017, viz, agouti (black?) ♀ 1035, when mated with albino ♂ 2059, produced 2 agouti > red, and 2 black > red young. This result indicates that ♀ 1035, like her mother, formed gametes, half only of which bore the agouti character, half the black character. But the black character is apparently present in ♀ 1035 as a simple recessive, not latent in recessive albinism as in her mother; for the mating of ♀ 1035 with albino ♂ 2059, though it produced 4 young, gave no albino offspring; and a subsequent mating with white > red-black (albino) ♂ 1631 likewise gave no albino offspring, but 1 agouti and 1 black-red young. This ♀ 1035 undoubtedly arose from the union of an agouti gamete furnished by the father (since he was shown by breeding tests to be pure) with a gamete bearing the black character furnished by the mother, ♀ 2020. But if ♀ 1035 does not contain recessive albinism, the gamete furnished at her formation by ♀ 2020 can not have been an albino gamete. It would seem then that ♀ 2020 furnished certain gametes bearing black, not latent in association with albinism, but active. If so, she must have borne two different pairs of contrasted pigment potentialities, viz, (1) centripetal pigmentation *vs.* albinism; (2) agouti pigmentation *vs.* black pigmentation; and she must have transmitted

* A character indicated thus in parentheses is present in a *recessive* condition.

†This symbol is used to indicate inequality in the extent of body areas of different character as regards pigment. Thus, white > red means an animal with more white than red fur on its body.

centripetal pigmentation associated either with agouti or with black pigmentation (for the latter combination ♀ 1035 is specific evidence), and albinism associated probably either with agouti or with black pigmentation (these of course being in a latent condition). It seems from this and other similar cases that *the regional distribution of pigments on the body* (centripetal *vs.* albino) *is something inherited independently of the specific character of the pigments formed.* Albinism *vs.* centripetal pigmentation forms one pair of alternative (Mendelian) characters; agouti *vs.* black pigmentation forms another pair. An animal like ♀ 2020, then, is a dihybrid as regards pigment characters, and should form in equal number gametes of four different sorts, viz, albino [black latent],* albino [agouti latent], centripetal agouti, and centripetal black. This idea is supported by Allen's (: 04) observations on mice, and finds frequent illustrations in these experiments.

Agouti x *red.*—I have made this mating between pure parents only once. Agouti ♀ 2019, mated with red ♂ 2054, produced 4 young, 3 of them agouti > red, 1 red > agouti > white. This result indicates a tendency of agouti to dominate over red, or at least to mask the presence of red. In this experiment, the mother, ♀ 2019, had a red hip patch. The occurrence of red and of white spots on the young was probably due to a mosaic character of certain of her gametes rather than to some peculiarity of the father, a self red.

One of the young produced by this cross, viz, agouti > red ♀ 1294, when mated with her red father, ♂ 2054, produced 6 young, 2 agouti > red, 1 red > agouti, 2 red-black, and 1 red, indicating segregation of the respective agouti > red, and red characters brought together in the previous generation, so as to allow of the formation of pure red gametes. The occurrence of two red-black young indicates that in some cases the agouti character may break up into isolated black and red under the influence of the cross.

Agouti x *albino.*—Pure agoutis mated with albinos of spotted or of unknown ancestry have produced only animals predominantly agouti-colored, though the offspring have in some cases had one or more of the typical color patches red or white, but never black or chocolate. The spotting with red or white was inherent in the agouti stock used.

It is probable that in no case did the albino parent in these crosses transmit latent agouti. This statement is based on the results of other crosses made with these same albino animals, as well as on an examination of their pedigrees. If this assumption is correct, there is seen in this experiment a strong tendency for the agouti character to dominate over other pigment characters contained latent in albino gametes; for every one of the 17 young was agouti-pigmented.

* Brackets will be used to indicate latent characters, just as parentheses to indicate recessive ones.

The matings made and their results are:

Parents.		Young.			
Gold. agouti.	Albino.	Agouti.	Agouti-red.	Agouti red-white.	Silver agouti-yellow-white.
Agouti ♀ 1030	♂ 635.....	2	3	..	...
Agouti > red ♀ 1029	♂ 2059...	...	3	...	...
Agouti ♂ 2017........	♀ 785.....	3	1	...	...
Agouti ♀ 2018.........	♂ 635.....	1	2	1	...
Agouti > red ♀ 2021.	♂ 635.....	...	...	...	1
Total...............	....	6	9	1	1

That an albino may transmit latent agouti is shown unmistakably by the following case. Albino ♂ 2060 was purchased from a breeder and his ancestry is wholly unknown to me. But I found on mating him with spotted females not of agouti parentage that a large proportion of his young were agouti-marked, and this proportion proves to be almost exactly one-half. Thus he has produced by 15 different females, which were spotted with black and red (and in some cases also with white), 19 young marked with agouti (in no case with solid black hairs on the body, though frequently with red or white ones) and 18 young marked with black but not with agouti. By the red or red-white females he has produced 3 agouti-marked and 3 black-marked young. The total pigmented young produced by matings with the spotted females are 22 agouti-marked and 21 black-marked, an approximation to equality as close as is possible with an odd number of young. The matings with red and red-white females show that all the gametes formed by ♂ 2060 bear the latent character black pigmentation, but that half his gametes transmit it in the agouti combination with red, half in the form of solid or segregated black.

If this interpretation is correct it should be possible by suitable matings of ♂ 2060 with his descendants, or of the latter *inter se*, to obtain albinos *all* of whose gametes would transmit latent agouti. This matter, it is hoped, can soon be given an experimental test.

In the foregoing case it seems necessary to assume the dominance of agouti pigmentation over the intermingled condition of black and red spots; indeed, all my experiments support that idea, except possibly those mentioned in discussing the agouti × black cross (p. 26). The alternative dominance which may have occurred in those cases is apparently exceptional, the rule being that agouti pigmentation dominates over black or black-red. Alternative dominance can scarcely be invoked to explain the results obtained from the matings of ♂ 2060, for it would fail to account for the black-red offspring in the matings with red or red-white females.

The following experiment likewise bears upon the point which is under discussion. Agouti ♂ 2017, mated with albino ♀ 785, produced 3 agouti and 1 agouti > red young (as stated on p. 29). The albino ♀ 785 was born of albino parents, but part of her grandparents and great-grandparents were spotted black-red-white, part of them albinos; none were agouti-marked. It seems probable, therefore, that the pigment characters latent in the gametes of ♀ 785 were in every case black-red. If so, her agouti young should contain recessive white with which black-red had been introduced as a latent constituent, and should, as explained on page 28, form in equal numbers gametes of four sorts, viz, agouti, black-red, albino [agouti latent], albino [black-red latent]. If two such sets of gametes be combined (as in mating these hybrid young), and all gametic unions prove equally fertile, their young should be, on the hypothesis that agouti is dominant over black-red, in the proportions 9 agouti to 3 black-red to 4 albino; but on the hypothesis that agouti and black-red are alternatively dominant, the young should be in the proportions 6 agouti to 6 black-red to 4 albino. That is, on one hypothesis, agouti young should be three times as numerous as black-red; on the other hypothesis, both sorts should be equally numerous. The result observed is 7 agouti to 3 black-red to 3 white, which certainly favors the hypothesis that agouti dominates over black-red, though the number of young is undesirably small.

The details of the experiment follow:

Parents.	Young.		
	Agouti.	Black-red.	Albino.
Agouti ♂ 1509 × Agouti ♀ 1508...........	3	2	3
Agouti ♂ 1509 × Agouti ♀ 1507...........	2	0	0
Agouti ♂ 1509 × Agouti > red ♀ 1510..	2	1	0
Total	7	3	3

Other matings of agouti ♂ 1509 support the hypothesis that agouti gametes dominate over black-red ones. Thus he was mated with three different albino females derived from the same black-red-white spotted stock as his mother. The gametes of these females undoubtedly transmitted the black-red, never the agouti character. On the hypothesis that agouti is dominant over black-red, the young produced by these matings should be in the proportions, 2 agouti to 2 black-red to 4 albino;

on the hypothesis of alternative dominance between agouti and black-red, the young should be in the proportions, 1 agouti to 3 black-red to 4 albino. The numbers observed are 2 agouti to 3 black-red to 5 albino—too few to be conclusive, but favoring the former hypothesis. On the whole it seems highly probable that agouti as a rule dominates over all other pigment combinations, but in the case of exceptional animals like ♀ 2020, page 27, black or black-red gametes may be formed which have a potency equal to that of agouti. This is an indication of individual prepotency like that discussed further on, under the heading, "Prepotency and Dominance."

Agouti synthetically produced.—An occasional animal with an excellent agouti coat may result from mating a red with a black individual. One such animal, ♂ 1178, tested as to the character of its gametes, apparently forms pure red and pure black gametes in approximately equal numbers, for mated with red females he has produced 3 red, 2 black, and 1 agouti young. His red gametes uniting with those furnished by the red females should produce red offspring, while his black gametes forming similar unions should produce either black or agouti young. Hence the result observed is exactly what we should expect, on the hypothesis that black and red have formed merely a temporary, not a permanent union in the agouti parent, and that the gametes formed by it contain either red or black, but not the two united in the agouti combination. What conditions, if any, can bring about a permanent union between segregated red and black my experiments do not as yet indicate.

THE BLACK TYPE.

My original black animals were obtained from Miss Soule. Bred *inter se* they produce only black offspring, though a few red hairs may usually be found by careful search somewhere on the body. The relation of black to agouti has already been discussed, so that we may pass immediately to its relations with red and with albinism.

Black × red.—The young produced by this cross have ordinarily a black coat, but of a reddish shade, as if the pigmentation of the black parent had been diluted with that of the red one; in other words, the characters of both parents show their influence in the offspring, which are not intermediate, only because black pigment is so much more opaque than red that the latter is scarcely visible. In other cases the weakening of the black pigmentation is seen in a restriction of the black pigmented areas, which then fall into the series of pigmented patches described on page 9, while red, or red and white together, fill up the intervening spaces. This results in the production of a black-red or black-red-white spotted animal. Or, thirdly, and less often still, the black and red may have the characteristic distribution which produces the agouti coat.

In detail, the matings which I have made under this category and their results are as follows:

Parents.	Young.		
	Reddish black.	Black > red.	Agouti.
♂ 2053 (black, but with a few red hairs) × red ♀ 755	...	4	...
♂ 2053 × red ♀ 2031	...	2	...
♀ 2013 (very deep black, without red hairs) × red ♂ 2054	2	...	1
Total	2	6	1

Hybrids of all three sorts show segregation in forming gametes, though as yet not exactly in the expected Mendelian proportions. Thus the two reddish-black young of ♀ 2013 by ♂ 2054, viz, ♀ 1179 and ♂ 1180, have given the following results when mated with red animals:

Parents.	Young.				
	Red.	Yellow.	Black-red.	Black-yellow.	Agouti.
Black ♀ 1179 × red ♂ 2054 (father of ♀ 1179)	2	...	1	...	2
Black ♀ 1179 × red ♂ 2004	2	...	2	...	...
Black ♂ 1180 × red ♀ 1073	3	...	4	...	...
Black ♂ 1180 × red ♀ 1278	3		1	...	...
Black ♂ 1180 × red ♀ 1279	1	2	...	1	...
Black ♂ 1180 × red ♀ 1286	2	...	...	...	...
Black ♂ 1180 × red ♀ 1307	4	...	...	...	...
Black ♂ 1180 × red ♀ 2026	2	1	1	...	...
Black ♂ 1180 × red ♀ 2027	5	1	...	...	...
Total	24	4	9	1	2
	28		12		

It will be observed that ♀ 1179 has given by two different red males as close an approximation as is possible to the expected equality of red young on one hand and of black or agouti young on the other hand. But her brother, ♂ 1180, has produced a most astonishing excess of red individuals, more than three times as many red young being recorded as black ones. It would seem to be a peculiarity of this animal to form red gametes either more numerous or more vigorous than his black ones, for red young are in excess in all his matings

except one, that with ♀ 1073. Another unexpected result is the production of *weakly* pigmented animals of the red type, *i. e.*, of yellows, and of one yellowish-black (or blue) individual, where we expect only red and reddish-black offspring. The first mentioned peculiarity of ♂ 1180 is possibly shared by other cross-breds between the black and red types. Thus black > red ♀ 1156, a daughter of black ♂ 2053 by red ♀ 755, gave the following result:

Parents.	Young.	
	Red.	Agouti.
♀ 1156 × red ♂ 2054............	1	1
♀ 1156 × red ♂ 2004	4	0

Again, reddish-black ♀ 3017, a daughter of the similarly pigmented ♀ 1179 by red ♂ 2054, gave by red ♂ 2004, three young, all red. The results thus far obtained by mating with red females the agouti ♂ 1178 (produced by the cross of black with red) have been previously given. They indicate that this hybrid forms red and black gametes in numbers approximately equal. Combining the results of all the matings made between an animal whose parents were red and black respectively, and red animals, we get 37 red (or yellow) to 14 black, blue, or agouti, where we should expect an equal number in each of the two general classes. Further experiments are needed to show whether the inequality thus far observed is a chance result which will disappear with larger numbers, or whether it is significant and will remain.

Several other black-red animals, which evidently contain recessive red, have produced, when mated with red animals, 8 black-red and 13 red young. The matings making up this total are as follows:

Parents.		Young.	
Black-red.	Red.	Black-red.	Red.
♂ 23........	♀ 3...........	0	2
♂ 23........	♀ 4...........	1	3
♀ 1227.....	♂ 1140......	0	1
♀ 1288.....	♂ 1140......	0	2
♀ 1448.....	♂ 1140......	4	1
♀ 1482.....	♂ 1140	1	1
♀ 1607.....	♂ 1140......	1	1
♂ 1165.....	♀ 1262.. ...	1	2
Total....	....	8	13

Again, black-red pigmented animals which contain recessive red (or else latent red, see p. 25) when mated *inter se* have produced young as follows:

Parents.	Young.		
	Black-red.	Red.	Albino.
Black-red ♂ 23 × black-red (albino) ♀ 1 A.	7	4	...
Black-red (albino) ♂ 89.1^a × black-red (albino) ♀ 1 A.	...	2	...
Black-red ♂ 23 × black red-white ♀ 51.2^b	3	4	...
Black-red (albino) ♂ 89.1^a × black-red-white ♀ 51.2^b.	4	...	...
Black-red (albino) ♂ 89.1^a × black-red (albino) ♀ 89.3^b.	1	...	1
Black-red ♂ 23 × black-red (albino) ♀ 89.3^b	6	...	...
Black-red ♂ 23 × black-red-white ♀ 209	1	1	...
Total	22	11	1

We should expect the black-red young to be three times as numerous as the red ones, but we find them only twice as numerous, yet the numbers involved are small, and the precise proportion observed probably not significant. Combining the results of all matings of black pigmented animals which are expected to produce red young we get a total of 105 young:*

	Black pigmented.	Red pigmented.
Observed	44	61
Expected	61	44

Black × *albino*.—As elsewhere stated, few, if any, of my black animals are entirely free from red pigmentation, and my albinos, so far as determined, always possess latent red. Accordingly, more often than otherwise, the young produced by this cross show more or less red pigmentation, though in my experiments it has never amounted to more than a few red hairs, or one or two small red spots situated at the border of one of the typical pigment patches. The blackest young produced in this series of experiments resulted from matings between a very heavily black pigmented female (♀ 2012) and an albino male (♂ 635) part of whose gametes, as stated on page 24, entirely lacked the black character.

* Further experiments made since the foregoing was written continue to give a steady excess of red animals and a corresponding deficiency of black ones.

In detail, the matings made are as follows:

Mating.	Parents.	Young.		
		Black.	Black > red.	Black > white.
(1)	Black ♀ 2012 x albino ♂ 635.....	7	1	1
(2)	Black ♀ 2012 x albino ♂ 2002....	...	2	2
(3)	Black ♀ 2014 x albino ♂ 2039....	...	3	...
(4)	Black ♀ 2014 x albino ♂ 2059....	..	3	...
(5)	Black >red ♂ 2053 x albino ♀ 807	...	4	...
(6)	Black >red ♂ 2053 x albino ♀ 766	...	5	...
	Total	7	18	3

The relation existing between the characters combined in this cross is one of simple Mendelian dominance, followed by segregation in the next generation, as is clear from the following matings:

Mating.	Parents.	Young.			
		Black.	Black > red.	Black > white.	Albino.
(7)	Black>white ♂ 1111 [born of mating (2) above] x albino ♀ ♀....................	...	4	4	9
(8)	Black>red ♂ 1256 [born of mating (6) above] x albino ♀ ♀....................	...	3	1	4
(9)	Black ♂ 1570 [born of mating (1) above] x albino ♀ ♀	6	2	...	6
	Total............	6	9	5	19
		20			

The hybrid males, it is evident, form in approximately equal numbers albino gametes and those bearing the centripetal type of pigmentation, and the latter transmit essentially the same kind of pigmentation as was possessed by the pigmented parent and the pigmented grandparent. This conclusion is further supported by the result of matings of hybrids *inter se*, as shown on the following page.

Parents.	Young.			
	Black.	Black > red.	Black > white.	Albino.
Black>red ♂ 1256 [mating (6)] × black>red ♀ 1194 [mating (5)]......	3	...	...	...
Black>red ♂ 1256 [mating (6)] × black>red ♀ 1196 [mating (5)]......	1	3	...	2
Black>red ♂ 1256 [mating (6)] × black>red ♀ 1255 [mating (6)]......	2	...	...	1
Black ♂ 1570 [mating (1)] × black> red ♀ 1194 [mating (5)]...............	...	2	...	1
Black ♂ 1570 [mating (1)] × black> red ♀ 1197 [mating (5)].............	...	2	...	1
Black ♂ 1570 [mating (1) × black> white ♀ 3024 [mating (7)]...........	...	1	2	1
Black ♂ 1570 [mating (1)] × black> white ♀ 3136 [mating (7)]...........	...	1	1	...
Total	6	9	3	6
	18			

The result observed is in exact agreement with the expected Mendelian ratio, 3 : 1.

From what was said on page 24 concerning the transmission of pigment characters by albino gametes, we should expect that the character of the albino used in a cross with black would in some measure influence the result of the cross. That this is actually so is indicated by comparing results of matings (1) and (2), page 35, the black parent being the same in both matings, but the albinos markedly different. One of the albino males (♂ 635) forms gametes about half of which are entirely free from black; the other (♂ 2002) always transmits black pigmentation, frequently with a tendency to spotting. By the former were produced nine young, all but two of which were self-colored black; by the latter were produced four young, all spotted with red or black.

THE RED TYPE.

Red (including its dilute forms known as yellow and cream) is the only one of the three pigments of the coat which I have been able to obtain unquestionably free from the other two. Red and yellow animals not only form no black pigment in their hair, but appear to be incapable of transmitting the capacity to form black coat pigment. Red animals mated *inter se* ordinarily produce only red offspring, but reds obtained by cross-breeding with black may produce yellows when bred *inter se*. This case will receive further attention presently. Yellow mated with yellow produces, in my experience, only yellow offspring.

The relations of red to agouti and to black have already been discussed, and in part also that of red to albinism. Accordingly it remains only to consider in greater detail the last-named topic.

Red × *albino.*—The result of this cross depends upon what latent pigment characters are borne by the albino, and this in turn may in some cases be inferred from the ancestry of the albino, though in other cases not. Most of the albinos with which I have experimented contain latent black as well as red, and when mated with red or yellow animals produce invariably black-pigmented offspring. The matings indicated in Table D fall into this category of cases.

TABLE D.—*Matings of albinos (all of whose gametes transmit latent black) with red or yellow animals. The pigmented offspring all have black pigment in their coats.*

Parents.		Young.				
Albino.	Pure red or yellow.	Black-red.	Black-yellow.	Gold agouti-red.	Silver agouti-yellow.	
Albino ♀ 644.. .	Red ♂ 2004.......	4	...	...	...	
Albino ♀ 761.....	Red ♂ 2004........	2	...	...	...	
Albino ♀ 778.....	Red ♂ 2004.......	3	...	...	..	
Albino ♀ 778.. ..	Red ♂ 2054.......	...	1	2	...	
Albino ♀ 779.....	Red ♂ 2004........	4	...	...	...	
Albino ♀ 1216 ...	Red ♂ 2054........	2	...	1	1	
Albino ♀ 1649 ...	Yellow ♂ 1347...	...	4	...	...	
Albino ♂ 2002	Red ♀ 755.........	3	...	...	...	
Albino ♂ 2002...	Red ♀ 784.......	2	...	...	...	
Albino ♂ 2002...	Yellow ♀ 2001...	...	3	...	...	
Albino ♂ 2039...	Red ♀ 753.........	4	..	...	...	
Albino ♂ 2039...	Red ♀ 830.........	4	..	...	...	
Total.........	....	28	8	3	1	
Albino.	Hybrid red or cream (albinism recessive).	Black-red.	Black-yellow.	Gold agouti-red.	Silver agouti-yellow.	Albino.
Albino ♀ "Himalayan."	Cream ♂ 1147....	...	3	...	...	4
Albino ♀ 766....	Cream ♂ 1147....	...	1	...	...	1
Albino ♀ 1027...	Red ♂ 1019......	2	...	...	...	1
Albino ♀ 1028...	Red ♂ 1019.......	...	...	2	...	4
Albino ♀ 1544...	Red ♂ 1433.......	2	...	...	...	...
Albino ♂ 2002...	Red ♀ 683.........	2	...	...	...	...
Albino ♂ 2039...	Red ♀ 1020.......	1	...	...	...	2
Albino ♂ 2060 ..	Red ♀ 1355.......	...	...	1	...	1
Albino ♂ 2060...	Red ♀ 1442.......	...	...	2	...	2
Albino ♂ 2060...	Red ♀ 1476.......	3	...	...	...	4
Total.........	....	10	4	5	...	19

Sixteen different albinos mated, as indicated in the table, with red, yellow, or cream animals, produced 59 pigmented young, all bearing black pigment.

Seven of my albino animals contain latent black, but transmit it apparently to only about half of their offspring. Matings of such albinos with red or yellow animals are enumerated in Table E.

The pigmented young produced by these matings are 41 black pigmented, 37 free from black pigment (*i. e.*, bearing only red or yellow pigment in their coats). The obvious explanation is that only *one* of the two gametes which united to form each of these albino parents contained latent black, the other being free from it; consequently only half the gametes formed by the albinos contain latent black.

TABLE E.—*Matings of albinos (part only of whose gametes transmit latent black) with red or yellow animals. Approximately half of the pigmented offspring have black pigment in their coats.*

Parents an albino and a pure red, red-white, or yellow animal.	Young.				
	Black-red.	Black-yellow.	Red.	Yellow.	Albino.
Albino ♂ 635 × red-white ♀ 43...	3	...	1	...	...
Albino ♂ 635 × red ♀ 470.........	2	...	...	...	...
Albino ♂ 635 × red ♀ 575.........	...	...	4	...	...
Albino ♂ 635 × red ♀ 610.........	2	...	...	...	...
Albino ♂ 635 × red ♀ 610 and red ♀ 753............	5	...	3	...	...
Albino ♂ 635 × red ♀ 755.........	...	...	1	...	...
Albino ♂ 635 × red ♀ 830.........	2	2	4	1	...
Albino ♂ 635 × red ♀ 1073. ..	...	...	1	...	...
Albino ♂ 635 × red-white ♀ 1093.	5	...	1	...	..
Albino ♂ 635 × red ♀ 2008.......	...	...	3	...	...
Albino ♂ 635 × yellow ♀ 2001...	...	2	...	1	...
Albino ♀ 815 × yellow ♂ 2061..	..	1	...	3	...
Albino ♀ 1222 × red ♂ 2004......	1	...	2	...	...
Albino ♀ 1222 × red ♂ 2054......	1 (agouti-red.)	...	1	1	...
Albino ♀ 1224 × yellow ♂ 1347....	...	1	...	2	...
Albino ♂ 1516 × red-white ♀ 1387	3	...	1	...	...
Total..................................	24	6	22	8	...
	30		30		•

Parents an albino and a red, red-white, or yellow animal with recessive albinism.	Young.				
	Black-red.	Black-yellow.	Red.	Yellow.	Albino.
Albino ♂ 635 × red-white ♀ 690..	1	...	1	...	1
Albino ♂ 1516 × red-white ♀ 1344.	2	...	...	...	2
Albino ♂ 1516 × yellow ♀ 1346...	...	2	...	...	1
Albino ♂ 1516 × yellow ♀ 1348....	...	2	...	...	...
Albino ♂ 1516 × red-white ♀ 1434.	1	...	1	...	2
Albino ♀ 1216 × red ♂ 1386........	...	...	1	...	...
Albino ♀ 1224 × red ♂ 1386........	1	...	3	...	...
Albino ♀ 1236 × red ♂ 1386........	2	...	1	...	...
Total..................................	7	4	7	...	6
	11		7		

A means of testing the validity of this explanation has been suggested by Allen (: 04) for the similar case of chocolate pigmentation in mice. If the albino gametes which contributed to the production of the red or yellow offspring in the matings last mentioned were really *free* from black, then two of these hybrid red animals (containing recessive albinism) when mated should produce albino offspring *not any* of whose gametes contain latent black. Experiment has shown this to be the actual result. Albino ♂ 1999 was produced by mating two hybrid yellow animals containing recessive albinism. He has been several times mated with yellow females (see Table F) and has produced 13 pigmented offspring, all yellow. As a control he was mated also with a black female containing recessive albinism. This mating produced 3 albinos and 1 *black* pigmented young. Another albino tested, ♂ 2059, is apparently similar in nature to ♂ 1999, for when mated with red ♀ 610, he produced 3 young, all red pigmented (see Table F). The ancestry of this albino is unknown to me, as I obtained him from a breeder, and as no other test of this sort was made in his case, the result can not be considered conclusive, because of the small number of young produced; but it is probable that all his gametes were free from latent black, for four of his albino daughters by albino mothers containing latent black form albino gametes free from black, as well as other gametes containing black. They are ♀♀ 1216, 1222, 1224, and 1236, Table E. Each of these four daughters of ♂ 2059, all that have been tested, must have received from the father albinism free from latent black, for the mothers, as stated, did not form gametes containing latent black.

TABLE F.—*Matings of albinos (not any of whose gametes transmit latent black) with red or yellow animals. Not any of the offspring are black pigmented.*

Parents.		Young.		
Albino.	Pure red or yellow.	Red.	Yellow.	Albino.
♂ 1999	Yellow ♀ 3105	...	3	...
♂ 1999	Yellow ♀ 3200	...	3	...
♂ 1999	Yellow ♀ 3085	...	5	...
♂ 2059	Red ♀ 610	3	...	...
Total		3	11	...
Albino.	Yellow (albinism recessive).	Red.	Yellow.	Albino.
♂ 1999	♀ 1346	...	...	3
♂ 1999	♀ 1348	...	...	2
♂ 1999	♀♀ 2063 and 3036.	...	2	1
Total		...	2	6

Although the discovery of the differences among albinos, as regards matings with red animals, was made by mere accident while comparing the matings of ♂ 635 with those of other albino males, I have since found it possible to produce at will albinos free from latent black (like ♂ 1999) by beginning with matings between ordinary albinos (all of whose gametes transmit latent black) and red or yellow animals. The following case illustrates the method used: Albino ♂ 2002 is shown by matings recorded in Table D to form only gametes transmitting latent black. For by red or yellow females he has produced 10 pigmented young, all with more or less black in their coats. From the mating with yellow ♀ 2001 there resulted 3 black-yellow young, ♀♀ 2033–2035. Each of these, according to the hypothesis offered, received from one parent albinism with latent black, and from the other yellow free from black. In forming gametes the yellow-black hybrids should produce gametes of four different kinds, all equally numerous (on the hypothesis that albinism is inherited independently of specific pigments,

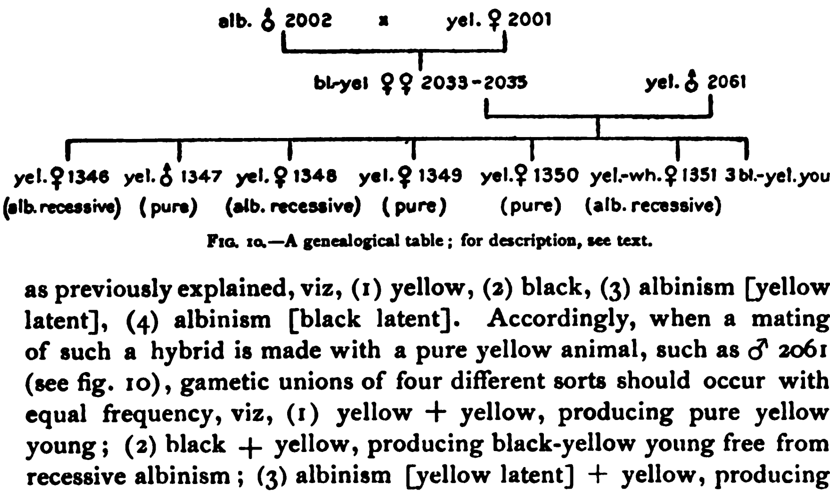

FIG. 10.—A genealogical table; for description, see text.

as previously explained, viz, (1) yellow, (2) black, (3) albinism [yellow latent], (4) albinism [black latent]. Accordingly, when a mating of such a hybrid is made with a pure yellow animal, such as ♂ 2061 (see fig. 10), gametic unions of four different sorts should occur with equal frequency, viz, (1) yellow + yellow, producing pure yellow young; (2) black + yellow, producing black-yellow young free from recessive albinism; (3) albinism [yellow latent] + yellow, producing yellow young (with albinism recessive); (4) albinism [black latent] + yellow, producing black-yellow young (with albinism recessive). That is, half the young should be yellow, half should be black-yellow; and of each sort half again should contain recessive albinism, half should be free from it. In the case under discussion (see diagram, fig. 10) there were produced 6 yellow and 3 black-yellow young, but in a series of matings equality of the two classes would undoubtedly have been more closely approximated, as Table E indicates. The yellow young alone were tested for the presence of recessive albinism, and it was found in exactly half of them, viz, ♀♀ 1346, 1348, and 1351, the test indicating that the other three yellow young are pure. The method by which

albinos free from latent black may be obtained from red or yellow hybrids, like ♀♀ 1346, 1348, and 1351, has already been explained. It is simply to mate the hybrids *inter se*, when there should be produced albino young, approximately one-fourth of all the young produced, and these albinos should be free from latent black. A number of albinos have been so produced in these experiments, but only one of them, viz, ♂ 1999, Table F, has yet been tested. It is evident that his gametes are, as expected, free from latent black.

This experiment indicates methods of practical utility to the breeder who desires either albinos as free as possible from peripheral pigment

TABLE G.—*Matings inter se of red or yellow animals having albinism recessive. None of the young black-pigmented. Expected proportion of albinos 1 in 4.*

Parents.	Young.		
	Red or red-white.	Yellow or yellow-white.	Albino.
Red ♂ 1019 × red ♀ 4	7	...	1
Yellow ♂ 1147 × yellow ♀ 1032	...	3	...
Yellow ♂ 1147 × yellow ♀ 1487	...	3	2
Yellow ♂ 1147 × yellow ♀ 1489	...	3	1
Yellow ♂ 1147 × yellow ♀ 1786	...	...	2
Yellow ♂ 1147 × red ♀ 2029	2	1	...
Red ♂ 1433 × red ♀ 1643	3	...	...
Red ♂ 1453 × red ♀ 1291	2	2	...
Red ♂ 1453 × red ♀ 1292	3	...	...
Red ♂ 1453 × red ♀ 1297	2	1	...
Red ♂ 1453 × red ♀ 1299	2	...	...
Red ♂ 1453 × red ♀ —?	4	...	...
Red ♂ 1477 × red ♀ 1292	3	1	...
Yellow ♂ 1998 × yellow ♀♀ 1351 and 1535	...	4	2
Total	28	18	8
	$\underbrace{\qquad\qquad}_{46}$		

or animals of various shades of red or yellow. For (1) albinos free from latent black have much less peripheral (chocolate or chocolate and black) skin pigment than others, and (2), when mated with red or yellow animals they frequently produce young of a *lighter* shade of red or yellow than that of the pigmented parent. He who mates ordinary albinos with red animals in hope of obtaining yellows will be sorely disappointed, for the young will be mottled with black (received latent from the albino parent); but he who employs albinos, such as I have described, in matings with red or yellow animals, may doubtless with patience realize his fondest hopes. By this method I have been able to produce cream-colored animals of a much lighter shade than any I ever saw before. Theoretically it should be possible by following up this method to produce animals practically white, but

with dark eyes. Time will show whether this is possible. It is not improbable that practical difficulties may be encountered. Experienced breeders say that the "purest" albino guinea-pigs (*i. e.*, those most free from peripheral pigmentation) incline to sterility. Two cases which have occurred in my own experiments make me think there is some truth in this idea. Further, albinos free from latent black have not yet been mated *inter se*, but I shall not be surprised

TABLE H.—*Matings of males mentioned in Table G with animals black pigmented, but having albinism recessive. The expected proportion of albinos is 1 in 4.*

Parents.	Young.				
	Black-red.	Black-yellow.	Yellow.	Agouti-yellow.	Albino.
Red ♂ 1019 × agouti ♀ 2020	2	...	..	...	...
Yellow ♂ 1147 × black-yellow ♀ 1149	...	...	...	...	3
Yellow ♂ 1147 × silver agouti-yellow ♀ 1252	...	..	1	2	...
Yellow ♂ 1147 × black-yellow ♀ 2034	...	1	1	...	...
Total	2	1	2	2	3
	7				

TABLE I.—*Matings of males mentioned in Table G with albino females. It is expected that half the offspring will be albinos.*

Parents.	Young.			
	Black-red.	Black-yellow.	Agouti-red.	Albino.
Red ♂ 1019 × albino ♀ 1025	...	...	2	4
Red ♂ 1019 × albino ♀ 1027	2	...	...	1
Yellow ♂ 1147 × albino ♀ "Himalayan"	...	3	...	4
Yellow ♂ 1147 × albino ♀ 1194	...	...	...	2
Yellow ♂ 1147 × albino ♀ 815	...	...	..	2
Red ♂ 1433 × albino ♀ 1544	2	...	...	...
Total	4	3	2	13
	9			

to find them relatively unproductive when this is done, for the hybrids bred *inter se* have in certain cases produced fewer *albino* young than they should produce on the Mendelian hypothesis. Thus, an examination of Table G shows that only 8 albinos have been produced in a total of 54 young, where 13.5 are expected. Nevertheless, this may be only a chance deviation from the expected proportion of albinos which will disappear as larger numbers are produced. Tables H and I indicate that the hybrid males employed in the matings enumerated

in Table G really produce a full quota of albino gametes, and that these are entirely fertile when they meet gametes transmitting black, either active or latent.*

It is a question of much interest, theoretical as well as practical, whether animals of a particular type, when produced by cross-breeding, form the same sort of gametes as are produced by pure-bred animals of the same type. In the case of albinos this evidently is not always true. From an albino which forms gametes all of which transmit latent black, there may be produced, as we have seen, by cross-breeding with a red animal and then interbreeding the hybrids, albinos of three different sorts as regards the transmission of latent black pigment. Again, the character of a red race which breeds true may be modified by cross-breeding with black, resulting in the production of yellow young. Thus two red animals, young of black (red recessive)

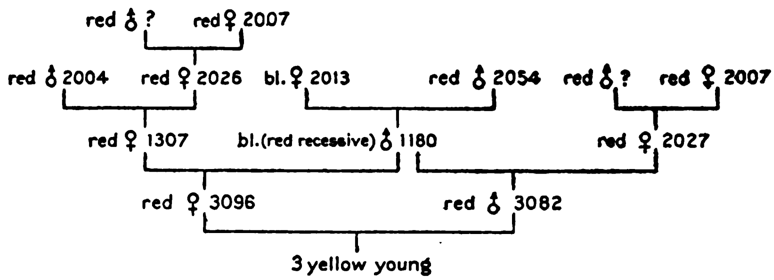

FIG. 11.—A genealogical table showing how cross-breeding between red and black may cause variation in the intensity of the red.

♂ 1180, by two different pure-bred red females, when mated together, produced a litter of 3 yellow young. The relationships involved will perhaps be more readily understood from the above diagram (fig. 11).

Apparently the cross with black induced variation in the intensity of the pigmentation transmitted by the gametes bearing red, so that some of the zygotes which were formed bore the dilute form of red, viz, yellow.

BLACK-EYED WHITE.

Guinea-pigs of this sort have hair and skin very free from pigment, indeed in the integument of the living animal I can detect no pigment at all, yet the eyes are black pigmented. Two animals of this sort have been born in the course of my experiments, and I have likewise experimented with two others obtained by purchase. They are not albinos and do not contain recessive albinism, at least those which I have had do not. They are of spotted parentage and may be considered spotted animals in which the typical pigment patches show an extreme

* Experiments made since the foregoing was written show that albinos free from latent black are entirely fertile *inter se*. Further, the deficiency of albinos observed at first is now disappearing.

condition of reduction. The successive steps by which the pigmentation of guinea-pigs undergoes reduction are about as follows: (1) The pigment centers are all functional, but the pigment areas do not quite meet along the middle of the ventral surface, or in the forehead. Perhaps the pigment fails to reach one or more of the feet also. (2) One or both shoulder patches are wanting, producing the Dutch-marked type (compare fig. 6, p. 12). (3) The side patches are also wanting; only the rump and sides of the head are pigmented (fig. 2, p. 10). (4) The rump patch disappears; only the sides of the head are pigmented, and here the patches are small, or one or more of them may be wanting (fig. 4, p. 11). An extreme condition of this sort is represented by ♂ 721, whose coat was entirely unpigmented except for a small patch of black about 5 mm. square on the outer surface of his right ear. (5) The skin is wholly unpigmented, though the eyes are as in all the foregoing stages dark. One can by selection progress in either direction through this series of changes, either increasing or decreasing the number and extent of the pigment patches, but it is impossible without long-continued selection to fix the color pattern at any particular stage in the series; perhaps it is wholly impossible to do so, as Cuénot (:04, p. LV) asserts on the basis of his studies on mice, but this I very much doubt. I doubt it first, because we do find color patterns of this sort firmly fixed in many wild species, such as antelopes, skunks, etc.; secondly, and still more, I doubt it because of what we see accomplished in domesticated animals. Take the case of cattle alone. Different breeds of cattle have often distinctive color patterns, as well as specific pigments in their coats. Holstein cattle are white, marked with large but more or less irregular black spots, the color pattern being apparently not definitely fixed. Dutch belted cattle, probably derived from the same general source as the Holstein, have for a long time been subjected to a rigid selection for a more definite color pattern, viz, an animal wholly black except for a broad white belt around the middle of the body. To this type the breed is said to keep very true.

Pure-bred Hereford cattle as kept at the present time in America are red over the greater part of the body, but are invariably white-faced; a longitudinal white stripe extends down the middle of the back, and the belly and flanks are more or less extensively marked with white. The white face, though now rigidly insisted upon and always seen in pure-bred herds, has not always been so common in the breed. A half century or more ago, according to Shaw (:03), rival breeders advocated white-faced and mottled-faced Herefords, but the former prevailed, and by continued selection the mottled-faced condition has now apparently been eliminated from the breed.

These cases indicate that certain of the typical color patches, as, for example, the cheek patches of cattle, can by continued selection be

eliminated altogether, while others are kept at their maximum intensity. How this is possible we could understand better if we knew in what condition pigment characters are transmitted in the germ. From the experimental evidence alone it would seem probable that the different color patches are represented in the germ by different elements separately heritable, possibly in different chromosomes—though of this we know absolutely nothing—and that as a result of long selection these separately heritable elements may become firmly associated with particular body regions. From the mode of development of the hair pigments as described by Leo Loeb ('97) and confirmed by observations of Mr. Howard and myself, it is clear that the pigments are formed in the Malpighian layer of the epidermis. A pigment patch, then, is, morphologically, simply the pigmented epidermis of a particular body region, and its character is determined by whatever determines the character of the epidermis in that body region.

That black-eyed white animals are essentially animals of the centripetally pigmented type is shown by breeding them *inter se* or by mating them with albinos. In every case thus far I have obtained only young with one to several, or even with *all*, of the typical pigment patches. The task of establishing a black-eyed white race which will breed true is similar to that of establishing a Dutch-marked race which will breed true, or in cattle a white-faced race like the Hereford. It is not to be accomplished in a single generation, but I doubt not its possibility. When guinea-pigs have been bred to a particular color pattern for many generations, we can form a better estimate of the magnitude of the task involved, and possibly meantime may learn something about the mechanism of transmission of the color patches.

The specific pigments transmitted by black-eyed white animals are probably determined by the same rules that govern in the latent pigmentation of albinos. These pigments probably differ according to the parentage in different cases, or more correctly according to the latent pigmentation which each individual received from its parents. Indeed, it is not impossible that vanished pigment patches are merely *latent* pigment patches, and that the reason why these keep reappearing in such a seemingly erratic fashion is that they keep emerging from latency under the influence of cross-breeding. In the black-eyed white animals with which I have experimented, red as well as black spots are apparently transmitted in the gametes formed, but I should expect that in animals different in origin red might be transmitted apart from black or *vice versa*.

I have not examined with the microscope the eye-pigments of the different self-colored varieties of the guinea-pig. From a superficial examination, however, I should say that black pigment is present in

every case except that of the albino. Yet we have seen that red and yellow animals, which have no black pigment in their coats, do not transmit black coat-pigment to their offspring, though they do transmit black eye-pigment. We might conclude that eye-pigment is something altogether different from and independent of coat-pigment, but two considerations negative this idea: (1) Black-eyed white animals mated with albinos produce animals with coat-pigment in the typical patches, a thing which neither parent possessed; (2) in mice, animals with coat patches but devoid of eye-pigment, when mated with unrelated albinos, produce offspring with pigmented eyes, again a character which neither parent possessed (Darbishire, :04). From these facts we see that a certain connection does exist between eye-pigmentation and coat-pigmentation, though apparently it is less close than that between one coat-patch and another coat-patch. The disappearance of eye-pigmentation, like the disappearance of coat-pigmentation, is probably due, in the case of ordinary albinos, to *latency* in the germ of a particular hereditary unit. This condition of latency, it is evident, can be made to disappear by cross-breeding with any animal of the centripetally pigmented type. But in centripetally pigmented animals, as we shall see, disappearance of eye-pigment, when once it has occurred, is apparently beyond recall, at least by cross-breeding with albinos. This is indicated by the instructive experiments of Darbishire (: 04), which we shall presently examine more in detail.

A condition which might be described as semi-latency of a coat-pigment was observed in the case of a red-white animal, ♀ 915, which was mated with red ♂ 1019. To my great surprise she produced in two successive litters four young having *black*-red coats. This was contrary to any previous experience (compare Table G), and I at once sought for an explanation. Upon looking the animal over carefully I found, what I had before overlooked, that she had a sacral patch of *black skin*, though not a single hair of her body, so far as I could discover, was black pigmented. The capacity to form black integumentary pigment was evidently present in the animal, though its influence extended only to the epidermis proper, not to the hair-follicles. One often sees in dogs, for example in fox-terriers, black skin spots of this sort in body regions where the coat is entirely white. The character semi-latent in ♀ 915 came into full activity in four of her offspring by a male devoid of that character.

Black skin is not infrequently seen on the feet of red guinea-pigs, but such animals do not produce young with black hairs when they are mated with other red animals. A comparison of this result with that described in the case of ♀ 915 serves to emphasize the distinction which has been made between centrifugal and centripetal pigmentation

(see p. 9). The black-footed guinea-pig has the former, which it transmits to its offspring; it does not possess the latter and its offspring never do, unless a mating has been made with an animal having pigmentation of that sort. The black-footed red guinea-pig, as regards black pigmentation, is in exactly the same condition as an albino with dark-pigmented extremities; centripetal black pigmentation is fully latent in it.

Black-eyed white animals, of the sort which I have had, and animals like ♀ 915, are centripetally pigmented animals in which the capacity to form black pigment in the typical central patches is *semi*-latent, *i. e.*, they may apparently transmit the character in a fully active condition, when mated *inter se*, a cross with animals having a different type of pigmentation being unnecessary for this purpose.

Darbishire's pink-eyed but centripetally pigmented mice, if they possessed at all the capacity to form eye-pigment, must have possessed it in a more than latent condition, for they bred true *inter se*, and though a cross with albinos brought the character into full activity, there are strong reasons for believing, as we shall presently see, that the capacity to form eye-pigment was recovered, not from the pink-eyed animal, but from the albino with which it was mated. It is to be expected that continued selection and inbreeding of black-eyed white guinea-pigs would establish a condition of the coat-pigment patches similar to that of the character eye-pigmentation in Darbishire's pink-eyed mice, a condition which goes beyond the latency of centripetal pigmentation in albinos, and may, for all we at present know, amount to elimination of the character in question from the germ. This question offers an attractive field for further investigation.

Comparison with pink-eyed mice.—The dark-eyed mice obtained by Darbishire (: 04) upon mating pink-eyed spotted mice with albinos, yielded an interesting result when bred *inter se*. Approximately one-fourth of the young were, as we should expect, albinos; one-half were dark-eyed, like their parents, the primary hybrids; and one-fourth were pink-eyed and spotted. We should naturally expect the dark-eyed young (like their parents) to contain recessive albinism, and the pink-eyed spotted ones to be free from it, like their pink-eyed grandparents. While in many cases this was undoubtedly true, in others it was not true; for Darbishire's breeding experiments show that some of the dark-eyed animals did not contain recessive albinism, and that some of the pink-eyed ones did. Further, the "extracted" albino young in some cases behaved differently from their albino grandparents in crosses with pink-eyed spotted animals. They produced pink-eyed as well as dark-eyed hybrids, the two sorts being approximately equal in number (7 pink-eyed to 6 dark-eyed, Darbishire, : 04, Table D, p. 24).

From this it is clear that the five albino parents which gave the result just described transmitted in approximately half their gametes the pink-eyed and in half the dark-eyed condition. These albinos are comparable in the matter of the pink-eyed character with my albino guinea-pigs of Table E in the matter of black coat-pigment. A close parallel exists throughout the two cases. Darbishire's original albinos all contained latent the character pigmented eye. This character was invariably brought into activity by a cross with the centripetally pigmented but pink-eyed race. That race would seem not to have possessed the character eye-pigmentation, even in a state of latency which a cross with albinos would bring into activity; for half the gametes formed by the hybrids apparently lacked the character eye-pigmentation, and that character was as often associated latent with the albino character, as it was associated active with the alternative character, standing for centripetal pigmentation. If so, the hybrids must have formed with equal frequency gametes of these four sorts: (1) pigmented coat, pink-eye,* (2) pigmented coat, dark-eye, (3) albinism [pigmented coat and pink-eye latent], (4) albinism [pigmented coat and dark-eye latent].

Hybrids forming sets of gametes like these, when mated *inter se*, should produce young visibly of three classes in the proportions, 9 dark-eyed pigmented to 3 pink-eyed pigmented to 4 albino. The numbers observed by Darbishire are 287 (or 284?) dark-eyed pigmented, 131 (or 134?) pink-eyed pigmented, and 137 albino young.

On the hypothesis which I have suggested, these young, though visibly of only three different sorts, should really fall into nine classes, whose numerical proportions are theoretically as follows :†

$$\left.\begin{array}{l}\text{Class (1), } 4\ P\,d\ (A\ p)\\ \text{Class (2), } 2\ P\,d\ (p)\\ \text{Class (3), } 2\ P\,d\ (A\ d)\\ \text{Class (4), } 1\ P\,d\end{array}\right\}\ \begin{array}{c}\text{9 pigmented}\\ \text{dark-eyed.}\end{array}$$

$$\left.\begin{array}{l}\text{Class (5), } 2\ P\,p\ (A\ p)\\ \text{Class (6), } 1\ P\,p\end{array}\right\}\ \begin{array}{c}\text{3 pigmented}\\ \text{pink-eyed.}\end{array}$$

$$\left.\begin{array}{l}\text{Class (7), } 2\ A\ [d\ p]\\ \text{Class (8), } 1\ A\ [d\ d]\\ \text{Class (9), } 1\ A\ [p\ p]\end{array}\right\}\ \text{4 albinos.}$$

This classification rests on the assumption that eye-pigmentation may be inherited apart from coat-pigmentation, *i. e.*, that the primary hybrids are really *di*-hybrids in the Mendelian sense. It involves the further hypothesis that eye-pigmentation was invariably latent in the original albino stock used, and as invariably absent from the pink-eyed

* Although the pink eye is due merely to *absence* of pigment from the eye, just as albinism to absence of pigment from the eye and coat, it is convenient in both cases to speak of the negative character as if it were positive. This can be done, I trust, without confusion to the reader.

† EXPLANATION.—A = albino; P = pigmented; d = dark-eyed; p = pink-eyed; ( ) indicate recessive characters, [ ] latent characters. The relative frequency of occurrence of individuals of each class is indicated by a coefficient.

pigmented animals (at least in a state capable of becoming active as a result of matings with albinos).

Let us now inquire whether Darbishire's experiments indicate the existence of these various hypothetical classes or not. Darbishire gives in the first part of his Table E, page 35, the results of mating *inter se* dark-eyed pigmented animals of generation F_2.* On the "ancestry" hypothesis these should all breed much alike, for their ancestry is similar in all cases; on the hypothesis which I have stated, they include the four distinct sorts of individuals which I have called classes (1) to (4), page 48, and these will breed very differently one from another. An examination of Darbishire's table shows that in fact the various pairs of pigmented dark-eyed animals gave results of four different sorts.

I. The following pairs gave young of three sorts—dark-eyed, pink-eyed, and albino:

Pair.	Young.		
	P d.	*P p.*	*A.*
2H 48.................	2	1	2
2H 52..................	3	1	1
2H 93..................	2	2	1
Total.	7	4	4

On the Mendelian hypothesis each of the parents in these three families must have furnished gametes bearing the pink-eyed character as well as gametes bearing the albino character. If so, and if each of these characters was represented in *half* the gametes formed, and the two characters were independent of each other, then the parents were of class (1), page 48, and the young should be as 9 *P d* to 3 *P p* to 4 *A*, which approximates roughly the observed 7 to 4 to 4.

II. The following pairs gave only dark-eyed and pink-eyed young, without albinos:

Pair.	Young.	
	P d.	*P p.*
2H 39α.................	5	2
2H 39β	4	1
2H 53β........	4	1
2H 139.................	4	1
2H 142...	6	2
Total...	23	7

* I adopt here and in the following pages Bateson's convenient notation for the successive "filial" generations following a cross, viz, F_1, F_2, F_3, etc.

A result of this sort can have followed either from matings *inter se* of animals of class (2), page 48, or from matings of such animals with those of class (1). In either case the young should be as 3 *Pd* to 1 *Pp*, a ratio closely approximated in the observed 23 *Pd* to 7 *Pp*.

III. The following pairs gave only dark-eyed and albino young, without pink-eyed pigmented ones:

Pair.	Young.	
	Pd.	*A.*
2H 50α	4	1
2H 50β	4	1
2H 53a	7	1
2H 96	6	1
2H 99	3	2
Total	24	6

Such a result would be produced either by mating *inter se* individuals of class (3), page 48, or by mating individuals of that class with those of class (1). In either case the young should be as 3 *Pd* to 1 *A*. The observed numbers, 24 to 6, are not greatly at variance with this ratio, considering the small number of young produced.

IV. The following pairs produced only dark-eyed pigmented young, without either albinos or pink-eyed pigmented young;

Pair.	Young. *Pd.*
2H 36	3
2H 49	6
2H 51	5
2H 92	3
Total	17

Such a result should follow mating *inter se* two individuals of class (4), page 48, or mating an individual of that class with one from any of the other three classes, (1) to (3), or from a mating between classes (2) and (3).

Accordingly, in the eighteen pairs which Darbishire formed of dark-eyed pigmented mice of this second filial generation (omitting only one pair which gave but a single young), we get evidence of the probable existence of all four of the hypothetical classes of dark-eyed individuals. If the pairs were taken quite at random without regard to the recessive characters present in the different animals (and this was evidently the case, since Darbishire does not admit the existence

of such characters), we should expect from the theoretical numerical frequencies of classes (1) to (4) that pairs giving the four sorts of results described would be as follows. The observed frequencies are for convenience in comparison given in a parallel column.

Group.	Expected frequency.	Approximately.	Observed frequency.
I	28	3	3
II	38	4	5
III	38	4	5
IV	53	6	4

The agreement between expected and observed frequencies, it will be noticed, is as close as could reasonably be expected in so small a number of pairs.

Again, Darbishire mated dark-eyed animals, like those whose matings we have been discussing, with dark-eyed animals of different parentage, one of the parents having been a hybrid, the other an albino. In all such cases the albino parent evidently possessed and transmitted to its offspring the dark-eyed character, for none of the pigmented young were pink-eyed. But the hybrid parent, according to our hypothesis, transmitted the pink-eyed character to half its offspring, forming gametes as follows (see p. 48) : $Pd + Pp + A\ [d] + A\ [p]$.

Union of the gametes of the albino parent, all $A\ [d]$, with gametes like these would produce young as follows:

$$Pd\,(A\,d) + Pd\,(A\,p) + A\,[d\,d] + A\,[d\,p].$$

But as Darbishire utilized in the experiment under discussion only pigmented animals, we are concerned at present only with the first two classes of young. They are identical in character with individuals of classes (3) and (1), respectively (p. 48), but occur in equal numbers, whereas in a group of hybrids like that described on page 48, class (1) is twice as abundant as class (3).

The question now before us is, if individuals of classes (1) and (3) be taken with equal frequency to mate with individuals taken at random from a mixture of classes (1) to (4) in the proportions indicated on page 48, what sorts of offspring are to be expected and in what proportions in the various pairs formed. Making the calculations by the methods already explained, we find that pairs should occur giving the same four sorts of results as in the previous case (pp. 49 and 50, I to IV); but these pairs should occur in frequencies somewhat different.

The pairs recorded by Darbishire (p. 35, Table E, middle section) which fall into these respective groups are as follows (omitting only one pair which produced 3 albinos and which might fall into either Group I or Group III):

GROUP I.

Pair.	Young.		
	Pd.	*Pp.*	*A.*
2H 23	2	1	2
2H 34	5	1	1
2H 38	2	3	1
2H 44ª	5	1	1
Total	14	6	5
Expected	9	3	4

GROUP II.

Pair.	Young.	
	Pd.	*Pp.*
2H 28	4	1
2H 33	5	1
2H 43	5	3
2H 107	3	3
Total	17	8
Expected	3	1

GROUP III.

Pair.	Young.	
	Pd.	*A.*
2H 29	3	1
2H 41	4	1
2H 44ᵝ	3	2
2H 101	5	2
2H 106	2	2
2H 119	4	2
2H 145	3	2
Total	24	12
Expected	3	1

GROUP IV.

Pair.	Young.
	Pd.
2H 32	5
2H 40	3
2H 103	5
2H 118	5
Total	18
Expected	all *Pd.*

The expected relative frequencies of these four sorts of pairs are as follows, the frequencies observed being given in a parallel column:

Group.	Expected frequencies.	Observed frequencies.
I	4	4
II	2	4
III	8	7
IV	4	4

From this experiment we get additional evidence of the existence of the four hypothetical classes of dark-eyed pigmented individuals, (1) to (4), page 48, and of their occurrence in something like the theoretical proportions. Still further support for this view is afforded by the third section of Darbishire's Table E, page 35, which includes matings of

dark-eyed animals, each having one albino and one hybrid parent. Half of these animals should have the character of class (1), p. 48, and half that of class (3). Pairs established by random selection of individuals should, therefore, be in the proportions, 1 mating within class (1) to 2 matings between classes (1) and (3) to 1 mating within class (3). Pink-eyed pigmented young should be produced only in matings of the first sort, but albinos should result from all three sorts of matings.

The matings which produced pink-eyed young are as follows:

Pair.	Young.		
	Pd.	*Pp.*	*A.*
2H 18	2	2	2
2H 27	4	1	...
2H 111	3	1	...
2H 116	...	4	2
2H 143	5	2	...
2H 146	3	3	1
2H 147	3	1	4
2H 148	4	5	...
Total	24	19	9
Expected	9	3	4

The remaining matings are as follows:

Pair.	Young.	
	Pd.	*A.*
2H 19	4	1
2H 20	5	2
2H 22	4	1
2H 25	1	3
2H 26	4	2
2H 37	3	3
2H 45	3	3
2H 110	3	...
2H 112	8	...
2H 113	2	3
2H 114	4	...
2H 115	3	1
2H 144	4	2
Total	48	21
Expected	3	1

The evidence from the group of matings contained in these two lists is less clear than that from the two groups previously examined. There is a considerable excess of pink-eyed young in most of the mat-

ings which produced offspring of that character, and a deficiency, almost as great, of albinos. If these deviations from the expected proportions indicate anything other than a chance result, it is an increase in the proportion of gametes bearing the character pink-eye associated with pigmented coat, and a corresponding diminution in the proportion of albino gametes. Yet such a change is of very doubtful occurrence; more probably the outcome is a chance one, for the deficiency of albinos produced by the eight pairs which had pink-eyed young is more than offset by an excess of albinos produced by the other thirteen pairs, the total young produced being 121 pigmented to 30 albinos.

The fact, too, that certain pairs of this category produced *no* albinos must not be taken as conclusive evidence that the animals mated did not contain recessive albinism. The expectation is that only 1 in 4 of the young produced will be albinos, and it is not surprising that, as a chance result, *no* albinos should be found among as few as the 3 to 9 young produced by a pair. More extensive tests, or the simpler test of mating with albinos, would without doubt have shown the formation of albino gametes by each of the parents in question, if they really were of the parentage indicated in Darbishire's table.

The foregoing considerations indicate that the correctness of the classification of pairs in the cases previously examined is not established beyond question. For example, a pair which in a total of 6 or 8 young has produced only those of two sorts, might in subsequent litters produce young of the third sort, which would place the parents in a different category. Only in the cases where young of all three sorts have been produced is the character of a pair conclusively established. In other cases the probability of correctness in the classification made increases with the number of young produced. Whatever errors are involved tend to increase the magnitude of Group IV (pp. 50 and 52) at the expense of Groups I to III, and that of II and III at the expense of I. Making all allowance for such possible errors, there would still seem to be little reason to question the existence, among Darbishire's dark-eyed mice of generation F_2, of all the four classes designated (1) to (4) on page 48.

The existence of the two classes of pink-eyed pigmented mice (5) and (6), page 48, is strongly indicated by matings *inter se* of pink-eyed mice belonging to generation F_2, as recorded by Darbishire in his Table H, page 37. According to our hypothesis, the pink-eyed mice of this generation are in character either Pp or Pp (Ap), individuals of the latter sort being twice as numerous as those of the former. Not any of them contain the dark-eyed character; consequently they should produce only pink-eyed young or albinos, when bred *inter se*. The

seven pairs tested by Darbishire produced 31 pink-eyed and 1 albino young, with no dark-eyed ones—conclusive evidence against the "ancestry" hypothesis of Galton and Darbishire, for all four grandparents were dark-eyed. The number of young produced by a pair in this experiment ranged from 2 to 6, the single albino occurring in a litter of 5. This one albino gives conclusive evidence that its parents both contained recessive albinism and so were of class (5). We should on the theory of probabilities expect the occurrence of *three* such pairs in seven taken at random. It is possible that more extensive tests would actually have shown the occurrence of more than this one, but it is a probability which amounts almost to a certainty that not *all* the seven pairs would have given albinos, had they been more extensively tested. If not, then the occurrence of individuals of class (6), *i. e.*, $P\,p$, would be fully established by the experiment. But the absence of recessive albinism from certain of the pink-eyed mice of this generation is shown in a simpler way, viz, by matings with albinos. Nineteen such matings are recorded by Darbishire in his Table G, page 36. The number of young produced by a pair ranges from 2 to 8. Five of the nineteen pairs produced albino young, showing that they contained recessive albinism and transmitted it in approximately half their gametes, for the young produced by these pairs are 12 pigmented to 12 albino. Since the remaining fourteen pairs produced not a single albino in a total of 74 young, it is certain that many if not most of them did not form albino gametes, for had they done so half their young should have been albino. The albino parents used in this test evidently all transmitted latent the black-eyed character, for every one of the nineteen pairs produced dark-eyed young, showing that the albino parent was either of class (8), page 48, or possibly of class (7). The occurrence of an albino of this latter class (one which transmits latent in half its gametes the dark-eyed character, but in the other half the pink-eyed character) is shown beyond question, in Darbishire's Table G, by a mating ($2H$ 120) which produced 2 dark-eyed and 1 pink-eyed young. The occurrence of albinos which may have been either of class (7), page 48, or of class (9) (*i. e.*, which transmitted the pink-eyed character either in half or in all of their gametes) is indicated by three pairs in Darbishire's Table F, page 36, as follows:

Pair.	Young.		
	Pd.	*Pp.*	*A.*
K 10	1	2	...
K 11	1	2	1
K 15	...	2	3

In this experiment the parents both belonged to generation F_2, and were respectively a dark-eyed animal—which might be taken from any of the classes (1) to (4), p. 48—and an albino—which might be taken from any of the three classes (7) to (9). We should, on the theory of probabilities, expect half the eighteen pairs enumerated in Darbishire's Table F as producing pigmented young to produce pink-eyed offspring. Only three, as stated, gave this result, instead of the expected nine. But the number of young produced by several of the pairs was very small, being in four cases 3, and matings which should produce less than 1 in 4 of pink-eyed young (viz, 3 in 16) may well have failed to produce any in litters of 4 or less. In the three matings cited it is evident that both parents formed gametes bearing the pink-eyed character, since pink-eyed young were produced. Accordingly the dark-eyed parent must have belonged either to class (1) or to class (2), and the albino parent either to class (7) or to class (9). In mating K 10, the dark-eyed parent was probably of class (2), since no albino young were produced, though the small number of young, three, leaves this uncertain; but in matings K 11 and K 15, it is clear that the dark-eyed parent was of class (1), since albino young were produced in both cases. There is nothing to indicate whether the albino parents in these three matings were pure or hybrid as regards the pink-eyed character, except the large proportion of pink-eyed young produced, which would indicate that they were probably of class (9), *i. e.*, pure.

Accordingly, in Darbishire's experiments, we lack strong evidence by breeding test of the occurrence of this class (9) only of all those indicated on page 48. Yet I doubt not that the single albino born of pink-eyed parents, as recorded in Darbishire's Table H, page 37, if tested would prove to be of this sort, *i. e.*, lacking entirely the dark-eyed character, so that when mated with pink-eyed animals only pink-eyed offspring would be produced. This result would be parallel with what in mice Allen (: 04) observed to be the relation of chocolate and chocolate-yellow pigmentation to albinism, and what I, in guinea-pigs, have shown to be the relation of red and of yellow pigmentation to albinism.

Heredity of Rough Coat.

In certain varieties of the domesticated guinea-pig the hair has a very peculiar arrangement, sloping away in all directions from certain points, which are situated for the most part symmetrically along the sides of the body, nearly coinciding with the centers of the typical pigment patches. As a consequence the animal seems covered with cowlicks or rosettes, between which the hair, sloping in opposite directions, forms a series of ridges or crests. These are best seen in the so-called Abyssinian (the short-haired but rough) variety. (See Pl. 2, figs. 3 and 4.)

When the rough coat character is best developed, rosettes are seen around the following paired centers: (1) The eye, (2) a point immediately behind the ear, (3) the shoulder, (4) a point dorso-lateral on the side of the body about midway between shoulder and hip, (5) the hip, (6) the groin, (7) each of the single pair of mammæ; and from two unpaired centers, viz, (8) the middle of the forehead, and (9) the navel. The direction of the hair is also reversed on the toes.

In crosses between pure rough individuals and smooth ones, the rough character is dominant, all the young being rough and ordinarily having the rough character as fully developed as in the rough parent. But certain smooth animals, which may properly be described as prepotent, produce offspring which show a weakened condition of the rough character, some of the typical rosettes being either less well developed than in the rough parent or wanting altogether (see Pl. 6, fig. 12). Such offspring may be called *partial rough*. They frequently transmit the rough character in its full intensity to their offspring, as we shall presently see, though they themselves are only partially rough.

Repeated crossing of rough animals with prepotent smooth ones results in further weakening of the rough character until it is almost eliminated. Successive stages in this weakening process may be recognized, which are about as follows:

Condition A: The fully developed rough character as above described (see Pl. 2, figs. 3 and 4).

Condition B: Forehead and shoulder rosettes have disappeared, hip and side rosettes either fuse into an obliquely longitudinal dorso-lateral part sloping downward posteriorly, or the hip center disappears entirely.

Condition C (Pl. 6, fig. 12): The only conspicuous rosettes are the side rosettes, though the ear rosettes may usually be found by careful examination; between the ear and side rosettes a ridge runs obliquely downward and backward across the body from the shoulder; there is likewise a median dorsal crest; the hair is reversed in direction on the hind feet, and turned laterally but not reversed on the front feet.

Condition D: Only a single pair of rosettes, the side rosettes, persist; a mid-dorsal crest extends from the head back to the rump; hair on the feet as in Condition C, or that of the front feet straight.

Condition E: No rosettes, a mid-dorsal crest from the head backward, perhaps half the length of the body; hair of toes reversed on hind feet only or not at all.

Condition F: No rosettes or crest. Hair reversed on hind feet only.

It must not be understood that these steps are necessarily taken one at a time. The original cross between rough and smooth may lead directly from Condition A to Condition D, when the smooth parent is very prepotent.

The matings which have been made between pure rough parents and smooth ones may be summarized as follows:

Parentage.	Young, in appearance.		
	R.	*PR.*	*Sm.*
R. ♂ 1516 × *Sm.* ♀♀	12	5	...
R. ♂ 1586 × *Sm.* ♀♀	8	...	...
R. ♂ 2002 × *Sm.* ♀♀	113	11	...
R. ♀ 2040 × *Sm.* ♂ 2060	2	..	...
R. ♂ 2059 × *Sm.* ♀♀	31	4	...
Total	166	20	...

[Abbreviations: *R.* = rough; *PR.* = partial rough; *Sm.* = smooth.]

It will be observed that every one of the 186 young produced by this experiment bears the rough character, all but 20 of them having it fully developed (Condition A); the character of the exceptional 20 partial-rough animals varies from Condition B to Condition D.

PREPOTENCY AND DOMINANCE.

The matings which produced the 20 partial-rough young are of particular interest. In detail they are as follows:

Parentage.	Young.		
	R.	*PR.*	*Sm.*
Sm. ♀ 208 (or 996?) × *R.* ♂ 2002	2	4	...
Sm. ♀ 2005 × *R.* ♂ 2002	...	5	...
Sm. ♀ 2005 × *R.* ♂ 2059	...	2	...
Sm. ♀ 2056 × *R.* ♂ 2002	4	2	..
Sm. ♀ 2056 × *R.* ♂ 2059	3	2	...
Sm. ♀ 1344 × *R.* ♂ 1516	1	3	...
Sm. ♀ 1499 × *R.* ♂ 1516	1	2	...

The partial-rough young, it will be noticed, were all produced by five (or possibly six) mothers. Unfortunately, there is some uncertainty as to the mother of the first of the lots of young enumerated. The two females (♀ 208 and ♀ 996) had 6 young together at the same time, and so it was impossible to separate the young by litters, but from the coloration and size of the young I think it probable that ♀ 208 was the mother of the 4 partial-rough young. But ♀ 996 was of the same smooth stock as ♀ 208, and it would not be surprising if her gametes had a similar potency. Unfortunately, no further tests with these mothers could be made, for they both died soon after producing the young enumerated. The two females, ♀ 2005 and ♀ 2056, were both mated with the same rough males (♂ 2002 and ♂ 2059). The former produced only partial-rough young by both males; the latter produced

some fully rough and some partial-rough young by both males. From these cases it seems clear that the production of partial-rough young was due to some unusual potency of the gametes bearing the smooth character, and that this potent character was inherent in *all* the gametes formed by ♀ 2005, but in only about *half* of those formed by ♀ 2056. If ♀ 208 was, as supposed, the mother of the 4 young, all partial-rough in character, then she probably formed only potent gametes, as did ♀ 2005 apparently; but if ♀ 208 and ♀ 996 each produced some of the partial-rough and some of the fully-rough young, then they were both similar in character to ♀ 2056, as regards the formation of potent gametes. It would seem probable, accordingly, that potency of the sort under consideration is a function of the gametes; that while most smooth females form *no* potent gametes, some form 50 per cent and some 100 per cent of such gametes; or, in other words, that some smooth animals are purely potent, others *hybrid*, as regards potency, but a majority *non*-potent.

The question now arises, is this potency handed on from generation to generation, *i. e.*, do the gametes remain pure as regards potency, or is their potency affected by a cross with the alternative and dominant character, rough coat. There is some evidence in favor of both these ideas. On one hand there is a manifest tendency for gametes to retain from generation to generation any abnormal potency which they may possess; but on the other hand cross-breeding probably does frequently alter the potency of recessive gametes.

The first of the two ideas just mentioned receives support from the admirable experiments of Coutagne (:02) with silk-moths, which seem to have received less attention than is warranted by their great richness in results and the care with which they have been executed. Coutagne crossed two distinct races of silk-moths, one of which produced only white cocoons, the other only yellow cocoons. Dominance apparently was alternative between the two characters, which seem to have been nearly equal in potency, so that sometimes one, sometimes the other dominated. The cocoons were 219 white in character, 240 yellow, without intermediates. Imagos hatching from either sort of cocoon, when mated *inter se*, produced the other sort of cocoon, as well as that from which they hatched, and approximately in the proportions 3 of their own sort to 1 of the other. Thus, moths hatching from white cocoons mated *inter se*, and moths hatching from yellow cocoons mated *inter se*, produced in different lots—

				TOTAL.
From white cocoons:				
White	339	87	180	606
Yellow	140	36	109	285
From yellow cocoons:				
White	120	34	80	234
Yellow	441	89	236	766

Evidently there is a strong tendency for white, when it dominates in a first cross, to behave as a dominant also among the progeny of that cross; and likewise for yellow, when it dominates in a first cross, to behave as a dominant among the progeny of that cross. This indicates clearly the persistence from generation to generation of relative potencies of gametes of a particular sort. As regards the relative proportions of white and of yellow cocooned young, it is noteworthy that there is throughout the experiment a slight excess of yellows over the expected, indicating a somewhat superior potency of that character, which, in matings between other white-cocooned and yellow-cocooned races, was found to be uniformly dominant.

That cross-breeding may modify the relative potencies of gametes seems highly probable, yet the evidence for this idea at present available is inconclusive. It consists principally in an observed excess of partial-rough young over the expected proportion in certain matings, which will presently be described, but the numbers of young as yet produced in these experiments are too small to be at all conclusive.

One mating of pure rough animals (*R.* ♂ 2002 × *R.* ♀ 2003) produced, as expected, only rough young, five in number (see p. 63).

Hybrid rough animals, *R.* (*Sm.*), when mated with pure rough animals, have produced, as expected, only rough young, 57 being fully rough (Condition A, p. 57) and 1 partial-rough (Condition B or C).

The one partial-rough animal occurred in a litter of three young borne by *R.* ♀ 2040 mated with hybrid *R.* (*Sm.*) ♂ 994. This female had previously borne two fully rough young by *Sm.* ♂ 2060 (see p. 58). It is probable, therefore, that the hybrid ♂ 994 did form some smooth gametes of unusual potency, though, unfortunately, he was not tested by other matings with rough females.

Hybrid rough animals, *R.* (*Sm.*) in character, when mated with smooth ones, have produced 127 rough young and 146 smooth ones, equality of the two classes being expected on the Mendelian hypothesis of segregation. Of the 127 rough young, all except 6 have Condition A, the fully rough coat. The 6 partial-rough young were produced in four different litters, each by a different pair. They were as follows:

Parentage.	Young, in appearance.		
	R.	*PR.*	*Sm.*
R. (*Sm.*) ♂ 1111 × *Sm.* ♀ 644	...	1	3
R. (*Sm.*) ♂ 1178 × *Sm.* ♀ 1661	1	1	...
R. (*Sm.*) ♂ 1332 × *Sm.* ♀ 1338	...	3	...
R. (*Sm.*) ♀ 2034 × *Sm.* ♂ 1147	...	1	1

The smooth animals used in these matings were all pure-bred except ♀ 1338, which had a hybrid, *R.* (*Sm.*), father, but a pure-bred smooth mother. We can not assume, however, that these hybrid rough animals formed in general weak rough gametes, for *R.* (*Sm.*) ♂ 1111 had in all, by smooth females, 13 rough offspring, but only in the mating with ♀ 644 was a partial-rough individual produced; again *R.* (*Sm.*) ♂ 1178 had rough offspring (6 in all) by three different smooth females, but only in the mating with ♀ 1661 did he produce a partial-rough animal. It would seem that the degree in which dominance is realized in the zygote is dependent upon the relative potency of the gametes uniting, and that potency is apt to be more variable in the gametes of cross-bred than in that of pure-bred animals. If so, hybrid rough animals bred *inter se*, or with cross-bred rough or smooth individuals, should produce an especially large proportion of partial-rough young. The experiments made are as yet hardly extensive enough to give a decisive answer to this question.

Fully rough hybrid, *R.* (*Sm.*), animals bred *inter se*, have produced in all 32 rough young, only one of which is a partial-rough. This one was produced by the following mating:

R. (*Sm.*) ♂ 1111 × *R.* (*Sm.*) ♀ 1438, produced 1 *R.*, 1 *PR.*, 2 *Sm.*

This same male, it will be remembered, produced a partial-rough individual by the smooth female 644.

We may return now to the question whether the condition of unusual potency in the smooth gametes of animals producing partial-rough young is handed on to the posterity of those animals. If the partial-rough character of hybrid animals is due simply to imperfectly realized dominance of the character borne by the dominant gamete, and if the characters united in the zygote maintain their distinctness and segregate with the same relative potencies, when gametes are formed by the hybrid as they possessed before, then we should expect to get fully rough, as well as partial-rough offspring, by mating partial-rough animals either *inter se* or with rough animals. The result of mating partial-rough with smooth animals would depend upon the relative potency of the gametes formed by the smooth mates; if *none* of their gametes were unusually potent, then the offspring should be half fully rough and half smooth, without partial-rough young. But if *half* the gametes formed by the smooth animals are unusually potent, then the offspring should be visibly as 1 *R.* to 1 *PR.* to 2 *Sm.*

Matings of these three sorts show the following results. The "expected" results are calculated on the hypothesis of persistent relative potencies and full segregation of the rough and smooth characters.

Parentage.	Young, in appearance.					
	Observed.			Expected.		
	R.	*PR.*	*Sm.*	*R.*	*PR.*	*Sm.*
I.—*PR.* (*Sm.*) × *PR.* (*Sm.*):						
♂ 1334 × ♀ 1267	...	2	1	...	...	...
♂ 1334 × ♀ 2029	1	2	...	...	...	...
♂ 1987 × ♀ 1268	1	2	1	...	...	...
♂ 1987 × ♀ 1269	...	1	2	...	...	...
♂ 1987 × ♀ 2007	...	3	...	...	...	...
♂ 1987 × ♀ 2008	2	...	2	...	...	...
Total	4	10	6	5	10	5
II.—*PR.* (*Sm.*) × *R.* (*Sm.*):						
♂ 1360 × ♀ 991	...	1	2	...	...	...
♂ 1360 × ♀ 1435	1	2	...	...	...	...
♂ 1631 × ♀ 1071	...	3	...	...	...	...
Total	1	6	2	4½	2¼	2¼
III.—*PR.* (*Sm.*) × (*Sm.*):						
♀ 1269 × ♂ 1024	...	1	2	...	...	...
♂ 1360 × ♀ 1327	...	1	1	...	...	...
♂ 1360 × ♀ 1506	1	...	3	...	...	...
♂ 1360 × ♀ 1595	1	...	...	...	...	...
♂ 1360 × ♀ 1596	...	1	1	...	...	...
♂ 1360 × ♀ 1859	...	1	1	...	...	...
♂ 1631 × ♀ 1029	1	...	...	...	...	...
♂ 1631 × ♀ 1035	...	...	2	...	...	...
♂ 1987 × ♀ 2107	...	...	3	...	...	...
♂ 1987 × ♀ 2119	1	...	...	...	...	...
Total	4	4	13	5¼ — 10½	0 — 5¼	10½

The agreement between the observed and the expected proportions of fully rough (*R.*) and partial-rough (*PR.*) offspring is sufficiently close to lend support to the hypothesis of persistent gametic potency from generation to generation. For on the alternative hypothesis, that partial-rough hybrid animals form only partial-rough gametes and smooth ones, no animals with the fully developed rough character should be formed either in Group I or Group III of the foregoing matings, but we see that young of this sort were produced in all these groups. Yet it is probable that cross-breeding must be recognized as an element which may modify the potencies of gametes, causing those of a cross-bred individual to be less uniform in potency than those of an animal not so crossed. Further experiments are needed to throw light on this question.

Leaving out of consideration the *degree* in which the rough character is developed in the coat of hybrid offspring, we may inquire how nearly the Mendelian proportions of rough and smooth young are approximated. This will be plain from an examination of the following table:

Nature of mating.	Young.			
	Observed.		Expected.	
	Rough.	Smooth.	Rough.	Smooth.
Rough × rough	5	...	5	...
Rough × rough (smooth)	58	...	58	...
Rough × smooth	186	...	186	...
Rough (smooth) × rough (smooth)	53	19	54	18
Rough (smooth) × smooth	135	159	147	147
Total	437	178	450	165
	615		615	

As in the case of albinism, there are a few more recessive individuals than are expected. This may be purely a chance result, or it may be due to superior fertility of the recessive gametes; but a different explanation is suggested by an observation which will presently be stated. The suggested explanation is that the excess of recessive individuals may be due to latency of the rough character in certain individuals apparently smooth. That such latency is possible is shown by the sudden appearance in one of my families of smooth animals of a partial rough individual, ♀ 969, having a well-marked crest extending from the head to the middle of the back and conspicuous though imperfectly developed side rosettes. The ancestors of this female for at least three generations had been ordinary smooth individuals, though it is possible that one or more of these may have had a slight crest in the region of the shoulders; for I found that a brother of ♀ 969, viz, ♂ 971, had such a crest, though it could be detected only by very careful examination. Unfortunately most of the ancestors had died before my attention was called to this case. The father's skin, which I have, shows no indication of a crest, though possibly it might have done so before it was dried. The partial-rough ♀ 969 had by the brother mentioned, ♂ 971, four young, one of which was a partial-rough like herself, the others being smooth. Clearly, then, she both possessed the rough character in a state of partial activity and was able to transmit it in this condition to her offspring, though in her ancestors it must have been present in a state of almost, if not quite complete latency. Very likely suitable matings of the mother would restore the rough character in certain of her offspring to a condition of full activity. Further experiments with this animal are now in progress.

If I have interpreted correctly the partial-rough animals obtained in my experiments, they may be similar in nature to centripetally pigmented animals which lack some of the typical pigment patches, or have only the eyes pigmented. A cross with albinos in which centripetal pigmentation is latent may serve to call the full set of coat spots into activity, producing fully pigmented young, as we have already seen. Similarly we may expect that crossing a partial-rough animal with a smooth animal in which the rough character is fully latent would call the rough character into full activity in the offspring. It remains, however, to demonstrate the existence of smooth animals containing *fully* latent the rough character. I have as yet no evidence of their existence other than the slight excess of smooth animals over the expected proportion.

Heredity of Long Coat.

The longest or contour hairs of ordinary domesticated guinea-pigs, like those of the wild *Cavia aperea*, do not exceed a length of about 4 centimeters, but domesticated varieties with hair many times that length are now well known. Where or when they originated is unknown; according to Cumberland they would seem to have been introduced into England from France; our American stocks probably came from England. Long-haired smooth animals are commonly called "Angoras," and long-haired rough ones "Peruvians." But the two sets of characters (long *vs.* short, and smooth *vs.* rough) are entirely independent of each other, as we shall see, so that for the present we shall consider only the length of the coat, irrespective of whether it is rough or smooth.

My first experience with long-coated guinea-pigs was wholly unpremeditated. In a family of short-haired guinea-pigs with which I was experimenting and was practicing close-breeding, there appeared several animals whose contour hairs were about twice as long as those of their parents. These animals were all descended from a single pair of short-haired guinea-pigs which had been purchased from a breeder, but which I have no doubt had numbered among their ancestors a long-haired animal. I found that the long-haired young bred true *inter se*, which indicated that the long-haired character was recessive in nature in relation to normal or short coat. This idea has been fully confirmed by subsequent experiments, which were systematically instituted with the longest haired animals which I could secure.

In studying the inheritance of this character, it is necessary to rear the young to an age of about two months before one can be sure whether they are to have a normal coat, or one of more than normal length. For at birth guinea-pigs of all sorts have hair of about the same length (2 cm.). The coat of short-haired guinea-pigs reaches its maximum length (about 4 cm.) not far from the age of one month, and

is then gradually shed. On the other hand, the hair of long-coated animals apparently is not shed at this period, but keeps on growing. At two months of age it is 5 to 7 cm. long, at three months it is 6 to 9 cm. long. In the period from three to four months of age is another critical stage. Animals which begin to shed their longest hair at this period apparently do not acquire a longer coat at any period of their subsequent life, but continue to have one whose maximum length is about 8 cm. But animals which pass the age of about four months without shedding their longest hairs increase the length of their coat rapidly, so that they may have a coat of 10 to 12 cm. maximum length when four to five months old, and one of 14 to 16 cm. at six to seven months.

The acquisition of an abnormally long coat is due, accordingly, not to unusually rapid growth of the hair, but to a peculiar mode of growth. The hairs of a normal animal are thick and stiff in the middle, but taper toward either end, somewhat like the quills of a porcupine. In the middle of the hair the medulla is very thick, but it diminishes gradually toward either end, where it is wanting altogether. A hair of this sort, then, is the result of a definite growth cycle in the hair follicle, this cycle covering apparently about two months' time, though my observations on this point are yet imperfect. When a hair is completed, after attaining a length of about 4 cm., a new one apparently is formed below it and crowds the old one out. But in the long-haired animal, the termination of a two-months growth cycle is frequently, if not regularly, omitted. The hair is more nearly of uniform thickness throughout its length, and is not narrowed to a base at the end of a single period of two months, but grows without interruption during two, three, or four such periods.

For this reason, as I have observed, hair measurements of long-coated animals do not form a continuous series, but tend to group themselves about mean maximal lengths as follows:

(1) 8 cm., double the length of normal or short coat, not attained under three months of age.

(2) 12 cm., three times the length of short coat; not attained under five months of age.

(3) 16 cm., four times the length of short coat; not attained under seven months of age.

Coats longer than this I have not had an opportunity to study, though such are said to occur.

That long-haired animals bred *inter se* produce only long-haired young is shown by the following experiment: Six different long-haired males (viz, 955, 1586, Pl. 5, fig. 9, 1709, 2002, Pl. 1, fig. 1, and 2060, Pl. 3, fig. 5) have been mated with 19 different long-haired females, producing 49 young, all long-haired. There were produced also seve-

ral young which died before their coat-character could be determined, but all those which survived had hair much longer than that of the ordinary short-haired animal.

Further evidence of the recessive nature of long coat is afforded by matings between long-haired and short-haired animals. Long-haired ♂ 2002 (Pl. 1, fig. 1), whose coat measures 14–17 cm., according to condition, has been mated with 14 different short-haired females, producing 58 young, all of which have hair under 5 cm. in length. Nevertheless, the influence of the long-haired parent is frequently seen in increased softness of the coat, though this is, as a rule, not longer than in the short-haired parent.

When two long-haired animals are mated, one of which has longer hair than the other, the offspring have a coat like that of the shorter-haired parent, usually without, though sometimes with, interspersed hairs of greater length (Pl. 6, fig. 11). In other words there is a strong tendency for the shorter coat to dominate in all cases over the longer one. Accordingly, evidence for the dominance of short coat in crosses with long coat is fairly complete; the evidence for the occurrence of segregation in the next generation is less satisfactory, for, though there occur among the offspring good long-coated and good short-coated individuals, others show a poor development of the long coat, and the whole number of long-coated animals exceeds that expected. Thus hybrids, *Sh.* (*L.*)* in character, mated *inter se*, have produced thus far 13 *Sh.* to 7 *L.*, where 3 *Sh.* to 1 *L.* are expected, and long-haired animals when mated with hybrids, *Sh.* (*L.*), for the most part children of ♂ 2002 (see Pl. 1, fig. 1) have produced 36 *Sh.* to 65 *L.*, or nearly twice as many long-haired as short-haired young, where equality of the two sorts is expected. These young have been born to seven different long-haired parents, and the excess of long-haired offspring appears among the young of all except two of them, as follows:

Parents.		Young.	
Long-haired.	Short-haired (*Long*).	Short.	Long.
♂ 206	♀ ♀ — —	5	5
♂ 732	♀ ♀ — —	5	9
♂ 1586	♀ 1698	0	4
♂ 1709	♀ 1730	2	1
♂ 2002	♀ ♀ — —	9	18
♀ 2040	♂ 994	0	3
♂ 2063	♀ ♀ — —	15	25
Total.		36	65

* *L.* = long-haired, *Sh.* = short-haired.

The departure here from the expected equality of the two classes is too great and too uniform to be referable to chance. It would seem probable, rather, that fewer gametes are formed bearing the character short-coat than are expected. This may be due either to failure of contrasted characters to segregate at gamete formation in certain cases, or possibly to partial latency of the character short-hair in gametes which transmit active the character long-hair, the resultant being an intermediate condition. Further experiments are needed to show which of these two ideas is correct, though at present the former seems more probable.

Short-haired females obtained by mating a primary hybrid, *Sh.* (*L.*), with a pure short-haired animal have, in several cases, been mated with the long-haired males, 2002 (Pl. 1, fig. 1) and 2060 (Pl. 3, fig. 5). It is expected that half of such females will contain recessive the character long-coat, and that half will be free from it, *i. e.*, will produce only short-haired young. The outcome shows that 9 out of 12 females tested contain recessive the character long-coat, for they produce long-coated young. This is another bit of evidence that segregation occurred less often than expected in the gametes of the primary hybrids, though it throws no doubt on the uniformly dominant character of short-coat. Again, the nine extracted hybrids, which contain recessive the character long-coat, should, when mated with long-haired animals, produce short-haired and long-haired young in equal numbers if segregation occurs in every case where it is expected. In the matings in question there have been produced 10 short-haired young and 16 long-haired ones—further evidence that segregation is less frequent than expected. It is true that these numbers are yet small, but their uniform deviation in one direction from the expected result indicates that they are significant. If so, we must recognize in this pair of characters full Mendelian dominance, attended, however, with only partial Mendelian segregation.

Correlation among Coat-Characters.

In the preceding pages we have discussed separately the heredity of three different pairs of alternative coat-characters which we have found to conform more or less closely with Mendel's law of heredity. It remains to inquire whether there is any correlation between one of these pairs of characters and another, *i. e.*, whether rough coat is more often associated with white or with pigmented coat, with long or with short coat, etc. An inquiry of this sort may be based upon experiments made with the albino male 2002 (Pl. 1, fig. 1), which possessed the recessive members of two of the pairs of characters (viz, albinism and long-coat), but the dominant member of the third pair (viz, rough coat). It goes without saying that he was pure as regards albinism

and long-coat, for all long-haired albinos are pure in these characters, and as the result of experiment it may be stated that he was likewise pure as regards the third or dominant character, rough coat. He was mated with nine different pure pigmented, short-haired, and smooth females, producing 29 young, all pigmented, short-haired, and rough (see Pl. 2, figs. 3 and 4), but, presumably, all containing the three corresponding recessive characters—albinism, long coat, and smooth coat.

He was likewise mated with three other pigmented short-haired, smooth females, which differed from those previously mentioned only in this, that they contained recessive albinism. They produced by this mating 15 young, of which all, of course, were short-haired and rough, but 9 were albinos and 6 pigmented. The latter should be similar in nature to the 29 young of the matings previously described, making in all, from matings of ♂ 2002, 35 young bearing the three dominant characters, but supposed to contain the corresponding recessives, *i. e.*, to be hybrid in all three pairs of characters. A number of these young which were tested by suitable matings proved to be of the character expected. They have produced by different matings all the eight possible visibly different combinations of characters, viz:

(1.) Pigmented rough short, *P. R. Sh.* (compare Pl. 2, fig. 4).
(2.) Pigmented rough long, *P. R. L.* (compare Pl. 5, fig. 9).
(3.) Pigmented smooth short, *P. Sm. Sh.* (compare Pl. 3, fig. 6).
(4.) Pigmented smooth long, *P. Sm. L.* (compare Pl. 5, fig. 10).
(5.) Albino rough short, *A. R. Sh.* (compare Pl. 2, fig. 3).
(6.) Albino rough long, *A. R. L.* (compare Pl. 1, fig. 1).
(7.) Albino smooth short, *A. Sm. Sh.* (compare Pl. 4, fig. 7).
(8.) Albino smooth long, *A. Sm. L.* (compare Pl. 4, fig. 8).

This result shows clearly that there is no *necessary* correlation between either character of one pair and either character of another pair. On the hypothesis that each pair of characters is, in its transmission, *wholly* independent of the others, *i. e.*, that no correlation whatever exists among the pairs, we should expect triple hybrids, like the 35 young of ♂ 2002 already described, to produce, when mated *inter se*, young visibly of the eight different sorts just enumerated in the following proportions: 27 *P. R. Sh.*, 9 *P. R. L.*, 9 *P. Sm. Sh.*, 3 *P. Sm. L.*, 9 *A. R. Sh.*, 3 *A. R. L.*, 3 *A. Sm. Sh.*, 1 *A. Sm. L.* It will be noticed that at least 64 young must be reared to an age at which all three coat-characters can be determined before we may expect all these classes to be represented among the offspring. As yet only 8 young have been reared to such an age, so that the results are scarcely significant quantitatively, yet they indicate that the classes which are expected to be largest will really be so, for the eight young are distributed thus: 4 *P. R. Sh.*, 3 *P. R. L.*, 1 *P. Sm. Sh.*

Certain of the triple-hybrid offspring of ♂ 2002 were mated in ways

other than *inter se*, which should give some indication of whether any correlations exist among the three pairs of coat-characters. Thus triple hybrids were mated with several pure pigmented, smooth, and short-haired individuals, *P. Sm. Sh.*, as follows:

Parents.		Young.	
P. (A.) R (Sm.) Sh. (L).	*P. Sm. Sh.*	Rough.	Smooth.
♂ 2036	♀ 972	...	3
♂ 2036	♀ 973	2	1
♂ 2037	♀ 906	3	...
♂ 2037	♀ ♀ 907 and 922	3	...
♂ 2037	♀ 915	2	1
♂ 2037	♀ 933	1	2
♂ 2037	♀ —	...	1
♀ ♀ 2033–5	♂ 2061	4	5
Total		15	13

All the young were, as expected, pigmented and short-haired. It is expected, further, that half will be rough, half smooth, and this result is approximated in the observed 15 rough to 13 smooth. The young, though visibly of only two sorts, should be—on the hypothesis that no correlations exist among the pairs of coat-characters—of eight different sorts, all equally numerous. For the gametes of the triple hybrids should be as follows: *P. R. Sh.* + *P. R. L.* + *P. Sm. Sh.* + *P. Sm. L.* + *A. R. Sh.* + *A. R. L.* + *A. Sm. Sh.* + *A. Sm. L.* But the gametes of the pure mates used should all be *P. Sm. Sh.*, and the zygotes formed (*i. e.*, the characters present in the young) should be with equal frequency of these eight sorts, parentheses indicating recessives not visible:

1. *P. R. (Sm.) Sh.*
2. *P. R. (Sm.) Sh. (L.)*
3. *P. Sm. Sh.*
4. *P. Sm. Sh. (L.)*
5. *P. (A.) R. (Sm.) Sh.*
6. *P. (A.) R. (Sm.) Sh. (L.)*
7. *P. (A.) Sm. Sh.*
8. *P. (A.) Sm. Sh. (L.)*

The tests to determine what recessives each of the young possesses are not yet complete, but thus far show the following distribution:

Class 1. 1 (or 2) individuals.
Class 2. 1 (or 2) individuals.
Class 3. 1 individual.
Class 4. None.
Class 5. 1 individual.
Class 6. 2 (or 3) individuals.
Class 7. None.
Class 8. 4 individuals.

Considering that only ten individuals have as yet been fully tested, their distribution among the classes is sufficiently wide to indicate the probable absence of correlation among the three pairs of coat-characters. The full details of the several tests on which this classification of individuals is based will be given in a subsequent report when a larger number of tests has been completed.

EXPERIMENTS WITH RABBITS.

Certain experiments with rabbits, while less extensive than those made with guinea-pigs, serve to confirm and extend some of the conclusions already reached.

CROSS BETWEEN TWO DIFFERENT TYPES OF ALBINOS.

Particularly instructive are the experiments with two different types of albinos, the pure or wholly unpigmented type, and the Himalayan or peripherally pigmented type.

A pair of Himalayans purchased of a dealer produced in two successive litters only good Himalayan young, 12 in number. Presumably, therefore, they were pure.

A pure white female rabbit born of pigmented parents, but herself wholly unpigmented, was likewise found to breed true when mated to animals like herself. Crosses were now made between the two breeds, as follows:

Parents.		Young.		
Pure white.	Himalayan.	Dark Himalayan.	Intermediate.	Mosaic.
♀ 1	♂ 6	2	3	1
♀ 1	♂ 7	1	2	3
Total		3	5	4

All the young had pigmented extremities; some were nearly or quite as heavily pigmented as those of the Himalayan parent, but others had pigmentation less heavy than that of the Himalayan parent; these we may call intermediate. Still others bore pigment on part only of the areas which are pigmented in a pure Himalayan; thus the foot might be pigmented, but its toes pure white, or the center of the nose white, with a sooty band lying above and to either side of it. Individuals such as this we may call mosaics. Dominance of the peripheral pigmentation was, accordingly, very imperfectly realized in the hybrid offspring. Nevertheless, segregation of the two types of albino character involved in this cross takes place with great regularity when the hybrids form gametes, and this is true alike of all three sorts of young, the dark Himalayan, the intermediate, and the mosaic, as the following matings show.

Parents.		Young.			
Hybrid.	Pure white.	Dark Himalayan.	Intermediate mosaic.	Intermediate.	Pure white.
Dark Himal'n ♀ 24.	♂ 56	...	2	...	2
Mosaic ♂ 20	♀ 1	...	1	2	3
Intermediate ♂ 19	♀ 51	1	...	2	2
Total		1	3	4	7
		8			

The observed result approximates equality of the pigmented and unpigmented classes of albinos, as expected on the hypothesis that segregation occurs in all cases. The one good Himalayan produced by the intermediate ♂ 19 is noteworthy as showing that the full Himalayan character was present in the hybrid and capable of segregation, though seen in a partially dominated condition in the hybrid himself. Similar cases occur in the matings enumerated below. Apparently cases of this sort are like those of the imperfect rough guinea-pigs produced by certain smooth animals in crosses with rough ones, which nevertheless were capable of transmitting the rough character in its full intensity.

Further evidence of segregation of the Himalayan and pure white types of albino character in the gametes of the hybrids is afforded by mating these *inter se*, as the following experiments show.

Parents.		Young.				
		Himalayan type.				P.
Hybrid.	Hybrid.	D.	D. M.	I. M.	I.	
I. ♂ 19	I. ♀ 21	1	1	1	4	...
I. ♂ 19	D. ♀ 23	...	...	...	1	...
I. ♂ 19	D. ♀ 24	2	...	2	...	3
D. M. ♂ 20	I. ♀ 21	1	1	2	...	3
D. M. ♂ 20	I. ♀ 22	2	...	3	3	1
D. M. ♂ 20	D. ♀ 23	3	1	...	...	...
		9	3	8	8	7
		28				
D. M. ♂ 20	I. ♀ 21	6				1
I. M. ♂ 45	D. M. ♀ 108	3				3
I. M. ♂ 45	D. ♀ 109	5				1
Totals observed		42				12
Totals expected		40½				13½

Explanation.—*D.* = fully pigmented or dark Himalayan; *D. M.* = dark mosaic; *I. M.* = intermediate mosaic; *I.* = intermediate; *P.* = pure white.

The observed numbers of Himalayan and pure white young, it will be noticed, approximate fairly well the numbers expected on the hypothesis of complete segregation.

The possibility of transmuting the Himalayan type into the pure white type by cross-breeding is suggested by an interesting experiment performed by Raspail (:02). He set at liberty in a park frequented by wild gray rabbits, a Russian female rabbit, which variety has the Himalayan type of peripheral pigmentation. The female was presumably fertilized by wild males, certainly by pure pigmented animals, as the outcome indicates. In three successive litters she produced only self-colored gray or black young, in numbers approximately equal, as follows:—

	Gray.	Black.
Litter 1	7	6
Litter 2	8	4
Litter 3	3	6
Total..........	18	16

Certain of the gray hybrids bred *inter se* produced 5 gray young, 3 white ones [apparently Himalayan], and 1 *pure white.* Two of the [Himalayan] whites, when mated *inter se* produced a litter of 4 [Himalayan] white young. Two of these in turn interbred produced 5 *pure white* offspring.

This experiment I attempted to repeat, substituting for the wild pigmented parent a pure reddish gray pigmented animal of the breed known as the Belgian hare. A female Belgian hare was mated with Himalayan ♂ 6, the original male employed in the experiments already described. Three young were reared, a male and two females, of a gray color somewhat darker than that of the mother, since it contained more black pigment. The hybrids bred *inter se* have produced young as follows:—

Parents.	Young.		
	Gray.	Black.	Himalayan.
♂ 48 × ♀ 49..........	2	(4?)*	3
♂ 48 × ♀ 50..........	5	1	1
♂ 48 × ♀ 50..........	5	3	2
Total..........	20		6

* Gray or black, died early.

It is expected that one-fourth of the young will be albinos, and this proportion is approximated. But all six of the albinos thus far obtained have pigmented extremities, as did their Himalayan grandfather. No pure whites have been produced. In this respect my results differ from those of Raspail. It is true that the intensity of pigmentation of these extracted Himalayans varies considerably, as does that of the pigmented young. There are dark and light Himalayans, just as there are dark and light grays, among the offspring. Cross-breeding has in this case, as in others, been the cause of variation within the types of the parents, but I have no evidence as yet that it can completely remove the pigmentation from the Himalayan albino type, thus converting it into a pure albino. Nevertheless further experiments may lead to this result, yet I hardly expect it in view of the distinctness shown by the Himalayan and the pure albino types in the experiments already described. I suspect, rather, that the Russian female, with which Raspail began his experiments, was in reality a hybrid, like those which I have described on page 70, in which *pure* albinism was recessive. Raspail says concerning her, page 172:

> La femelle de Lapin russe qui m'a servi pour mes expériences, n'était pas de race pure: le museau, l'extrémité des pattes, les oreilles et le dessus de la queue étaient d'un noir moins franc et moins velouté; sa taille était notablement plus forte et ses yeux rouges indiquaient qu'elle tournait à l'albinisme.

This explicit statement and description certainly favors the idea that she was a cross-bred with a *pure* albino race, which, if true, would fully explain the occurrence of pure albinos in her offspring of generation F_2, without necessitating the conclusion that the peripherally pigmented type of albino had been transmuted into the unpigmented type by cross-breeding.

HEREDITY OF LONG OR "ANGORA" COAT.

This character is in rabbits, as in guinea-pigs, a recessive Mendelian character. Dominance and segregation both appear to be complete in crosses between normal (or short-haired) and angora (or long-haired) rabbits. I have observed in this case neither formation of intermediates, *i. e.*, of inferior long-haired specimens, nor deviation from the expected proportions of long-haired and short-haired individuals, of which conditions there were some indications in guinea-pigs. But in one or two cases I have thought that I could recognize in hybrids a greater softness of the coat, just as in guinea-pigs which are cross-breds between long-haired and short-haired races.

The numbers of young thus far reared are small, and not much weight is to be attached to them, so far as quantitative results are concerned.

In detail the matings made are as follows:

Parents.		Young.	
Long.	**Short.**	**Short.**	**Long.**
♂ N	♀ ♀ 17, 18, and 28	10	...
♂ 45	♀ Lop	8	...
Total		18*	...
Short (L.)	**Short (L.)**	**Short.**	**Long.**
♀ 1	Brother	4	2
♀ 1	♂ 20 (son)	5	1
♀ 21	♂ 20	6	2
Total		15†	5
Long.	**Short (L.)**	**Short.**	**Long.**
♂ 45	♀ 108	2	4
♂ 35	♀ 109	4	2
Total		6‡	6

* Expected, all short. † Expected, 3 short : 1 long. ‡ Expected, 1 short : 1 long.

EXPLANATION.—L. = long-haired or angora. Parentheses indicate recessive characters not visible.

HEREDITY OF LOP-EARS.

Some experiments are likewise in progress with the inheritance of the large or lop-eared character in rabbits, but these are hardly far enough advanced to make their outcome certain. The young produced by a cross between two breeds having ears of different relative size themselves have ears of an intermediate size. In other words, there is no evidence of dominance. A second generation of young has been obtained, but is not yet fully grown; apparently they too will have ears of an intermediate character. If so, we may conclude that segregation as well as dominance is wanting in this case, which would seem to be one of blended or non-Mendelian inheritance, similar to that of the willow-hybrids studied by Wichura and that of the Hieracium hybrids of Mendel ('70).

SUMMARY.

(1) There occur among domesticated guinea-pigs three pairs of alternative coat-characters which conform in their inheritance to Mendel's law of heredity. These are (1) albinism, which is recessive with respect to pigmented coat; (2) smooth coat, which is recessive with respect to rough coat; and (3) long coat, which is recessive with respect to short coat. Two of the recessive characters, viz, albinism and long coat, are doubtless characters of comparatively recent origin, which have made their appearance since the guinea-pig was domesticated. The third recessive character, smooth coat, is undoubtedly ancestral, and curiously enough is regularly dominated by rough coat, a character probably of recent origin, for a cavy bearing rosettes like those of the "Abyssinian" guinea-pig is unknown in a wild state. This indicates that ancestral characters are not necessarily dominant over new characters in heredity. The three pairs of characters are probably wholly uncorrelated.

(2) In rabbits occur two of the three pairs of alternative coat-characters which are found in guinea-pigs. Here, too, albinism and long or "angora" coat are recessive characters. A rosetted or rough coat is unknown in rabbits.

(3) A sharp distinction must be made between characters which are recessive and those which are latent. Recessive characters disappear from an individual in which they are associated with the corresponding dominant character, yet they reappear distinct in half the gametes formed by that individual; latent characters are characters normally dominant, which have disappeared in recessive gametes beyond hope of recall, except under conditions of cross-breeding which are in most cases not entirely clear. Albino gametes transmit in a latent condition both specific pigment characters and specific color-patterns. These latent characters can be brought into activity only by cross-breeding with a pigmental animal. The rough coat-character may likewise become almost completely, if not quite completely, latent in smooth animals. These facts indicate a possible explanation of the observed slight excess of recessives over the Mendelian expectation in cases involving one or the other of these two pairs of characters. In the case of the long *vs.* short pair of characters, an excess of recessives and the occurrence simultaneously of intermediates in generation F_2, but not in F_1, are more probably due to imperfect segregation than to latency of the dominant character. It is possible, however, that *partial* latency and imperfect segregation are related, if not identical phenomena.

(4) Some recessive individuals are prepotent, for their gametes, when united with those of ordinary dominants, produce young of an intermediate character. These intermediates, however, have the power to transmit the full dominant character in matings with recessive individuals. There is reason to believe, accordingly, that the dominant character is in such cases, not partially latent, but partially ***dominated***. If so, we have in cases if this sort something remotely resembling the alternative dominance seen in certain of the crosses among silk moths made by Coutagne (: 02).

(5) The lop-eared condition in rabbits is probably a non-Mendelian character in its relation to normal ear; for the children and grandchildren produced by crosses are apparently alike intermediate in character.

(6) A cross between two different types of albino rabbits, Himalayan and pure white, shows imperfect dominance of the Himalayan character in the offspring, but complete segregation among their gametes.

(7) Cross-breeding between dominant and recessive individuals may lead to the production of new sorts of individuals in a variety of ways, *e. g.*, (1) by producing new combinations among different pairs of alternative characters, as among the children of triple-hybrid guinea-pigs; (2) probably by causing a complex character, like the agouti coat of guinea-pigs, to break up into its elements—black, chocolate, and yellow—one or more of the elementary pigment characters either becoming latent or passing bodily out of the gamete; (3) by the coming into activity of elements of the dominant character which were latent in recessive gametes, as black latent in albino guinea-pigs or in Himalayan rabbits (see next report); (4) by inducing variability in the intensity of characters, quite aside from resolution and recombination of characters, as when red cross-bred with black produces a very light shade of red, *e. g.*, yellow or cream.

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FIG. 1.—A LONG-HAIRED, ROUGH, ALBINO GUINEA-PIG, ♂ 2002.

Pure (*i. e.*, homozygous) as regards all three coat-characters, two of which are recessive in nature, one dominant. Fanciers' name for all animals of this appearance, whether homozygous or heterozygous in character, White Peruvian.

FIG. 2.—A SHORT-HAIRED, SMOOTH, RED GUINEA-PIG, ♀ 1355.

Pure in respect to two of its coat-characters, viz, smooth coat and pigmented coat, but heterozygous as regards the third, since it contains recessive long coat, though its own coat is no longer than that of most pure short-haired animals. Toes of right fore foot white. Fanciers' name for animals of this appearance, whether or not homozygous, Red English.

FIG. 3.—A SHORT-HAIRED, ROUGH, ALBINO GUINEA-PIG, ♂ 1095.

Son of ♂ 2002 (fig. 1, pl. 1) and of Red English ♀ 3, which contained recessive albinism, but was otherwise homozygous (compare fig. 2, pl. 1). This animal is a double heterozygote, containing recessive the two characters, long coat and smooth coat. As regards albinism, it is, of course, pure. Fanciers' name for all animals of this appearance, White Abyssinian.

FIG. 4.—A SHORT-HAIRED, ROUGH, BLACK-RED PIGMENTED GUINEA-PIG, ♂ 2037.

Son of ♂ 2002 (fig. 1, pl. 1) and of *pure* Red English ♀ 755 (compare fig. 2, pl. 1). A triple heterozygote containing recessive the three characters, long coat, smooth coat, and albino coat. The black pigment seen in this animal's coat was inherited, not from the red pigmented mother, but from the albino father. Unfortunately black areas are scarcely distinguishable from red ones in the figure. Fanciers' name for all animals of this appearance, Tortoise-shell Abyssinian.

FIG. 5.—A LONG-HAIRED, SMOOTH, ALBINO GUINEA-PIG, ♂ 2060.

From inspection alone of this animal, one may know that it is pure as regards coat-characters, since it manifests the three which are by nature recessive. Fanciers' name, White Angora.

FIG. 6.—A SHORT-HAIRED, SMOOTH, RED-BLACK PIGMENTED GUINEA-PIG.

The parents were both triple heterozygotes (compare fig. 4, pl. 2). This animal is, of course, pure as regards smooth coat, but whether it contains the two recessive characters which it does *not* manifest, can be determined only by breeding tests. In this figure, as in fig. 4, black areas unfortunately are indistinguishable from red ones. Fanciers' name for all animals of this appearance, whether pure or heterozygous, Tortoise-shell English.

FIG. 7.—A SHORT-HAIRED, SMOOTH, ALBINO GUINEA-PIG, ♀ 1499.

Daughter of two albino parents, viz, ♀ 991, a double heterozygote like ♂ 1095 (fig. 4, pl. 2), and ♂ 635, a pure short-haired, smooth animal. We know without experimental test that this animal is pure as regards the two recessive characters which it manifests, smooth coat and albinism, but breeding tests are necessary to show whether or not it contains recessive the character long coat. This animal has been found to form *prepotent* smooth gametes. Fanciers' name for all animals of this appearance, White English.

FIG. 8.—A LONG-HAIRED, SMOOTH, ALBINO GUINEA-PIG, ♀ 1756.

Daughter of ♂ 2060 (fig. 5, pl. 3) and of ♀ 993, which was a double heterozygote like ♂ 1095 (fig. 3, pl. 2). This animal, like ♂ 2060, being a triple recessive, is pure as regards all three coat-characters. Fanciers' name, White Angora.

FIG. 9.—A LONG-HAIRED, ROUGH, BLACK-WHITE SPOTTED GUINEA-PIG, ♂ 1586

Son of ♂ 2002 (fig. 1, pl. 1) and of ♀ 1067, which was a spotted triple heterozygote (compare fig. 4, pl. 2). We know without breeding tests that this animal is pure as regards the character long coat, the recessive which it manifests. Breeding tests have established the fact that it is pure also as regards the rough character, but heterozygous as regards pigmented coat, since it produces albino offspring when mated to albinos. Fanciers' name for all animals of this appearance, "Broken-color" Peruvian.

FIG. 10—A LONG-HAIRED, SMOOTH, SPOTTED AGOUTI-RED-AND-WHITE GUINEA-PIG, ♂ 1709.

Son of ♂ 2060 (fig. 5, pl. 3) and of ♀ 1105, a triple heterozygote (compare fig. 4, pl. 2). This animal manifests two recessive coat-characters, long coat and smooth coat, in regard to which it is, of course, pure, but it is heterozygous in respect to the third pair of coat-characters, for it produces albino as well as pigmented offspring, when mated to albinos.

FIG. 11.—A PARTIALLY LONG-HAIRED, ROUGH, AND SPOTTED GUINEA-PIG, ♀ 2258.

Daughter of two triple-heterozygotes (compare fig. 4, pl. 2). The long-haired character is imperfectly developed in this animal, only *part* of the hair being long as in the Peruvian grandparent, ♂ 2002 (fig. 1, pl. 1).

FIG. 12.—A TRIPLE HETEROZYGOTE, ♂ 1989a.

(Compare fig. 4, pl. 2.) Son of ♂ 2002 (fig. 1, pl. 1) and of black-eyed white ♀ 2005, which is also a prepotent smooth animal. The coat is in part pigmented; the rough character is imperfectly developed, showing only one pair of the rosettes which are typically formed (compare figs. 3 and 4, pl. 2).

Heredity of Coat Characters in Guinea-Pigs and Rabbits

BY

W. E. CASTLE
Assistant Professor of Zoölogy, Harvard University
Associate, Station for Experimental Evolution

PUBLISHED BY THE CARNEGIE INSTITUTION OF WASHINGTON
FEBRUARY, 1905